BOTANICAL MUSEUM LEAFLETS

HARVARD UNIVERSITY

PRINTED AND PUBLISHED AT THE
BOTANICAL MUSEUM
CAMBRIDGE, MASSACHUSETTS

BOTANICAL MUSEUM LEAFLETS

HARVARD UNIVERSITY

VOLUME XIX

BOTANICAL MUSEUM
CAMBRIDGE, MASSACHUSETTS
1959–1962

TABLE OF CONTENTS

NUMBER 1 (August 18, 1959)

The Phytomer in Relation to Floral Homologies in the American *Maydeae*
By WALTON C. GALINAT 1

NUMBER 2 (January 27, 1960)

Prehistoric Bean Remains from Caves in the Ocampo Region of Tamaulipas, Mexico
By L. KAPLAN AND R. S. MACNEISH 33

NUMBER 3 (May 19, 1960)

On the Origin of the Orchidaceae
By LESLIE A. GARAY 57

NUMBER 4 (June 30, 1960)

Cytological Observations on Two Tropical Forms of *Tripsacum*
By Y. C. TING 97

NUMBER 5 (June 30, 1960)

Prestonia: An Amazon Narcotic or Not?
By RICHARD EVANS SCHULTES AND ROBERT F. RAFFAUF 109

A Reputedly Toxic *Malouetia* from the Amazon
By RICHARD EVANS SCHULTES 123

NUMBER 6 (January 9, 1961)

How Were the Glass Flowers Made?
A Letter by Mary Lee Ware 125

NUMBER 7 (February 17, 1961)

The Hallucinogenic Fungi of Mexico: An Inquiry into the Origins of the Religious Idea among Primitive Peoples
By R. GORDON WASSON 137

NUMBER 8 (April 11, 1961)

Further Archaeological Evidence on the Effects of Teosinte Introgression in the Evolution of Modern Maize
By WALTON C. GALINAT AND REYNOLD J. RUPPÉ 163

NUMBER 9 (June 30, 1961)

Carludovica palmata in Broommaking
By MELVIN LEE BRISTOL 183

Neonelsonia—A Colombian Folk Medicine
By MELVIN LEE BRISTOL 191

Novelties in the Orchid Flora of the Guayana Highlands
By CHARLES SCHWEINFURTH 195

NUMBER 10 (May 7, 1962)

Edible Fruits of Solanum in South American Historic and Geographic References
By VICTOR MANUEL PATIÑO 215

Edible Fruits of Solanum in Colombia
By RICHARD EVANS SCHULTES AND RAFAEL ROMERO-CASTAÑEDA 235

INDEX OF ILLUSTRATIONS

PLATE

Apostasia nuda *R. Br. ex Wallich* XV

Carludovica palmata *Ruiz & Pavon* . . XXV, XXVI

Carludovica palmata. Fibres (text fig.), p. 184

Duckeella alticola *C. Schweinf.* XXVII

Epidendrum radiatum *Lindl.* XIX

Habenaria distans *Griseb.* XVIII

Maydeae. Cross sections of axes IV

Maydeae. Cupule and rachis segment III

Maydeae. Vascular systems in pistillate rachis . . II

Octomeria cordilabia *C. Schweinf.* XXX

Octomeria dentifera *C. Schweinf.* XXX

Octomeria filifolia *C. Schweinf.* XXX

Octomeria flaviflora *C. Schweinf.* XXX

Octomeria lancipetala *C. Schweinf.* XXX

Octomeria nana *C. Schweinf.* XXX

Orchidaceae. Crosses XIV

Orchidaceae. Embryogeny X

Orchidaceae. Evolution XIII

Orchidaceae. Floral Diagrams VIII

Orchidaceae. Gynostemium XII

Orchidaceae. Pollen grains (text fig.), p. 63

Orchidaceae. Seeds XI

Orchidaceae. Types of Placentation IX

Paphiopedilum Wilhelminiae *L. Wms.* XVI
Phaseolus coccineus *L.* VII
Phaseolus vulgaris *L.* . . . . . VI,VII
Ponthieva ovatilabia *C. Schweinf.* XXXI
Rudolph Blaschka, facing p. 130 XXII
Sobralia speciosa *C. Schweinf.* XXVIII
Solanum alibile *R. E. Schultes* XXXII
Solanum georgicum *R. E. Schultes*
XXXIII,XXXIV,XXXV
Solanum liximitante *R. E. Schultes* XXXVI,XXXVII
Solanum muricatum *Ait.*
XXXVIII,XXXIX,XL,XLI
Solanum platyphyllum *H. & B.* XLII
Solanum quitoense *Lam.* XLIII
Solanum Topiro *H. & B.* XLIV,XLV,XLVI,XLVII
Stelis latisepala *C. Schweinf.* XXIX
Stelis obovata *C. Schweinf.* XXIX
Tripsacum australe *Cutler & Anderson* . . XX,XXI
Tripsacum laxum *Nash* XX
Vanilla planifolia *Andr.* XVII
Zea Mays *L.* Archaeological maize from
Cebollita Cave XXIII
Zea Mays *L.* Cross section of pulvinus V
Zea Mays *L.* Manifestations of the phytomer . . . I
Zea Mays *L.* Teosinte introgression in Cebollita
Cave maize XXIV

INDEX

TO GENERA AND SPECIES

a-meé-má-ra, 254
ADACTYLUS, 62,70
AGAVE
  spp., 184
alkaloids, 110,111,116,123,153
AMANITA
  muscaria, 142,155
Amaranth, 36–38
AMARYLLIDACEAE, sens. lat., 60
APHYLLORCHIS, 77
APOCYNACEAE, 109,111,117,118, 124
APOSTASIA, 61,62,64,70,72, 85
  nuda *R.Br. ex Wall.*, 67,71, 89
  odorata *Bl.*, 86
  papuana, 72,73,96
Apostasioideae, 62,64,65,70, 72,74–76,78–80,83,85,86,89
ARCTOSTAPHYLLOS
  pungens, 165
ARISTOLOCHIA, 64,112
arracacha, 191,221
ARRACACIA, 192,193
  elata *Wolff*, 192
  Pennellii *Constance*, 192,193
  Wigginsii *Constance*, 192,193
  xanthorhiza *Bancroft*, 191
asna-lulo, 216
ayahuasca, 109,110,112–116, 120
badoh, 152
badoh negro, 152
bamboo, 6,7
BANISTERIA, 117
  Caapi, 110,116
BANISTERIOPSIS, 109,112, 113,115–118,120
  Caapi, 110,113–116,119,124
ba-rá, 284
be-beñ, 284
be-tá-ka, 223,280
beans, 33,34,37–40,54,55,223
  archaeological, 33–56
  common, 35,36,38,40,42–45, 52–55
  lima, 38,40,42,53
  runner, 35,36,38,40,45,48–51,55
  sieva, 40,53,54
  tepary, 54
beñ, 249
bo-po, 223
BONATEA, 76
BURMANNIA
  longifolia, 85
BURMANNIACEAE, 84,85
caapi, 109,112,113,115–117, 119,120
caapi-pinima, 116–119
cabuya, 184
cachon, 225,227
cachuma, 225,229

CALOPOGON
pulchellus, 71
caña-antigua, 98
CAPSICUM, 35
CARLUDOVICA
palmata *Ruiz & Pav.*, 183–189
CATTLEYA, 83
CEPHALANTHERA, 72,77,80
alba, 66,67,73,96
chaqui-lulo, 216
che-how-ke-noo-roo, 249
chicle, 124
chili pepper, 35–38
chonta-ruro, 216
CLAVARIA
truncata *Quél.*, 159
CLAVICEPS
spp., 153
CLEISTES, 77
CLEOME
serrulata, 165
cobuía, 278
cocona, 224,225,241,280,284, 286
COIX, 6
COLLETOTRICHUM
Lindemuthianum, 43
CONOCYBE
siligineoides *Heim*, 159
CONVOLVULUS
indicus Mill., 152
rubrocoeruleus (Hook.) D. Dietr., 152
venustus Spreng., 152
violaceus Spreng., 152
CORDICEPS
capitata (*Holmsk.*) *Link.*, 159
corn, 35–38,52,55
corn-grass, 5,6
CORYCIUM
crispum, 73,96
cotton, 36–38
CRANICHIS
crumenifera, 72,73,96
cubíu, 276
cubiyú 276
cuchara-caspi, 124
cucumber, 225–230
CUCUMIS
sativus *L.*, 225,229
CUCURBITA
Pepo, 35,38,52
moschata, 36,37
mixta, 37
CURCULIGO, 85
CYPHOMANDRA
betacea (*Cav.*) *Sendt.*, 235
Cypripedioideae, 62–66,68,70, 74–76,78–80,82,83,85,86
CYPRIPEDIUM, 64,68,74,80
Calceolus *L.*, 73,86,96
de-twa, 280
DENDROBIUM, 83
Diandrae, 78
DICTYOPHORA
phalloidea *Desv.*, 159
DIDYMOPLEXIELLA, 72
DISA
unifolia, 82
DUCKEELLA
alticola *C.Schweinf.*, 195–198
e-tó, 249
e-to-pa-a, 279

ELAPHOMYCES
granulatus *Fr.*, 159
variegatus *Fr.*, 159
EPIDENDRUM, 83
ciliare *L.*, 87
radiatum *Lindl.*, 93
EPIPACTIS, 68
EPISTEPHIUM, 70,77
ERIAXIS, 65
ERYTHRODES, 72,75
GALEOLA, 70,72,77
altissima, 71
glass flowers, 125–136
GOODYERA, 68,75
pubescens, 71
gourd, 35–38
HABENARIA, 76
distans *Griseb.*, 92
HAEMADYCTION
amazonicum, 109,117
HAEMODORALES, 80
hallucinogenic fungi, 137–162
HEVEA, 123
ho-moo-mé, 284
huevo de tigre, 224
HYPOXIDACEAE, 60,84
HYPOXIS, 60,61,85
ingo-sha-hush, 191,192
IPOMOEA
Hookeri G.Don, 152
puncticulata Benth., 152
rubrocoerulea Hook., 152
tricolor Cav., 152,153
violacea *L.*, 152,153
iraca, 183
Kerosphaeroideae, 61,63–65,
68,75,77–80,82–84,87,93
ko-bu-ya, 279
kö-mö-he-ro-ya, 249
le-tó, 284
le-tó-ma-ta, 254
LECANORCHIS, 65,77
javanica, 66,67
LAGENARIA
siceraria, 35
LEGUMINOSAE, 39
LILIACEAE, 60
LILIALES, 80
LIMODORUM, 72
abortivum, 66,67
LISTERA, 68
loo-poo-po-ró-la, 254
llullu, 216
llullu-ruru, 216
lulo, 216,217,220–223,236,237,
240,249,271,275,280,286
lulo de perro, 275
lulo morado, 275
LYCOPERSICON
esculentum *Mill.*, 235
ma-rá, 284
ma-ré-da, 284
ma-sha-kvé, 216,270
maize, 1–8,12,14,16,18,20,22,
23–30,37,97,100–102,106,
221,223
archaeological, 163–181
(See corn)
MALOUETIA, 123
furfuracea *Spruce*, 124
nitida *Spruce*, 124
peruviana *Woodson*, 124
Tamaquarina, 118,123,124
MALPIGHIACEAE, 111

mancadera, 277
MANIHOT, 49,118
dulcis, 38
MASCAGNIA, 112
Maydeae, 1,14,16,26
melon pear, 257
MELONGENA
laurifolia, 256,258,259
Microspermae, 68
Monandrae, 78
mushrooms, 137–162
narangitas de Quito, 221
naranja, 219
naranji, 222
naranjilla 216–224,241,270,271 274
narcotics, 109–122,137–162
NEONELSONIA, 191–193
acuminata (*Benth.*) *Coult. & Rose*, 192–194
ovata *Coult. & Rose*, 192
NEOTTIA, 68
Neottioideae, 61,63–66,68,70, 72,74,75,77,79–86,91
NEUWIEDIA, 61–63,72,78, 84,85
NEVROPHYLLUM
floccosum (*Schw.*) *Heim*, 159
NICOTIANA, 38
Tabacum *L.*, 235
'nti sitho, 146
OCTOMERIA
cordilabia *C. Schweinf.*, 204, 208,209,210
dentifera *C. Schweinf.*, 205, 208,209
filifolia *C. Schweinf.*, 206,208, 209
flaviflora *C. Schweinf.*, 207–209
lancipetala *C. Schweinf.*, 208–210
nana *C. Schweinf.*, 208,209, 211
parvula *C. Schweinf.*, 205
ODONTOGLOSSUM, 83
ololiuqui, 151,152
Ophrydoideae, 61,63–65,68, 74–84,87,92
OPHRYS
Nidus-avis *L.*, 87
opuntia, 35,36
ORCHIDACEAE, 57–96,195–214
ORCHIS
Morio *L.*, 87
ORNITHOGALUM, 60
palm, 223
PANAEOLUS
campanulatus var. *sphinctrinus* (Fr.) Bres, 160
fimicola (*Fr.*) *Quél.*, 160
sphinctrinus (*Fr.*) *Quél.*, 160
PANICUM, 36,38
PAPHIOPEDILUM, 68,82,83
Wilhelminiae *L. Wms.*, 90
pee-pee-ká, 249
pepino, 225–229,255–257
pepino dulce, 225
pepino morado, 255
pepino redondo, 255
pepo, 255
PHARBITIS
rubrocoeruleus (Hook.) Planch., 152
violacea (L.) Bojer, 152

PHASEOLUS, 40
acutifolius var. latifolius *Freeman*, 54
coccineus, 40,42,44–52,54, 55
lunatus, 40,42,44,46,54,55
polyanthus *Greenm.*, 51,52
spp., 53
vulgaris, 35,39–42,44,46,47, 52–54
PHRAGMIPEDIUM, 65
longifolium, 66,67
plantain, 221
po-ró-la, 284
POGONIA, 77
pomas de perro, 277
PONTHIEVA
diptera *Linden & Reichb.f.*, 214
ecuadorensis *Schltr.*, 214
ovatilabia *C. Schweinf.*, 211–214
poom-ka, 284
PRESTONIA
amazonica, 109–111,114–120
PROTORCHIS
monorchis *Massal*, 57
PSATHYRELLA
sepulchralis *Sing.*, *Smith & Guzm.*, 160
PSILOCHILUS, 72
PSILOCYBE
acutissima *Heim*, 160
aztecorum *Heim*, 160
caerulescens *Murr.*
var. mazatecorum *Heim*, 160
fma. heliophila *Heim*, 160
fma. ombrophila *Heim*, 161
var. nigripes *Heim*, 161
caerulipes (*Peck.*) *Sacc.*
var. Gastonii *Sing. & Smith*, 161
candidipes *Sing. & Smith*, 161
cordispora *Heim*, 161
cubensis (Earle) Singer, 162
fagicola *Heim & Caill.*, 161
Hoogshagenii *Heim*, 161
isauri *Singer*, 161
mazatecorum Heim, 160
mexicana *Heim*, 161
mixaeensis *Heim*, 162
muliercula Sing. & Smith, 159,162
semperviva *Heim & Caill.*, 162
Wassonii *Heim*, 159,162
yungensis *Sing. & Smith*, 162
zapotecorum *Heim*, 162
var. elongata *Heim*, 162
pumpkin, 35–37
puscolulo, 216,218,220
puscolulu, 216
RICINUS
communis *L.*, 218
RIVEA
corymbosa (*L.*) *Hallier f.*, 152,153
ró-ya, 284
Rudolph Blaschka, 125–136
RUTACEAE, 111
SATYRIUM, 60,61,74,78
saxicolum, 73,96
SELENIPEDIUM, 61,62,65, 70
Chica, 67,71
SOBRALIA
speciosa *C. Schweinf.*, 198, 200,201

Weberbaueriana *Kränzl.*, 199
Solanum, 235,236,267
alibile *R.E.Schult.*, 236–240
angulatum Ruiz & Pav., 267
angulosum, 221
esculentum, 222
galeatum, 221
georgicum *R.E.Schult.*, 220, 240–247
hyporhodium *A.Br. & Bouché*, 284,286
liximitante *R.E.Schult.*, 248–252,276,279
muricatum *Ait.*, 225,227,230, 254–266
var. *popayanum* Bitt., 225
peruvianum, 221
platyphyllum *H. & B.*, 266–269,276
quitense, HBK., 267
quitoense *Lam.*, 215,216,220, 221,225,240,241,267,270–275
var. septentrionale *Schult. & Cuatr.*, 217,221,222, 274,285
sessiliflorum *Dunal*, 275,276
sisymbrifolium *Lam.*, 276
straminifolium *Jacq.*, 249, 276,278,279
Topiro *H. & B.*, 220,222–224, 237,240,241,276,279–286
tuberosum *L.*, 235
variegatum *Ruiz & Pav.*, 229, 256,260,261
SPIRANTHES, 68,72,75
squash, 36,37,55
STELIS
latisepala *C. Schweinf.*, 199, 203
lentiginosa *Lindl.*, 202
obovata *C. Schweinf.*, 202,203
parvifolia *Garay*, 202
STROPHARIA
cubensis *Earle*, 162
sunflower, 37–38
tapaculo, 277
teo-nanácatl, 146
teosinte, 1–3,10,11,14,16,18, 24–29,37,38,163–178
TEREIETRA
violacea (L.) Raf., 152
TETRAPTERYS, 112,119
methystica, 119
topiro, 223,224
topirú, 280
TRIPSACUM, 1,3,14,16,18, 24–27,30,97,99
australe *Cutler & Anderson*, 98 99,101–106
dactyloides *L.*, 2,14,16,18,97
floridanum, 100
latifolium, 98
laxum *Nash*, 97–103,106
pilosum, 98
spp., 163
tumo, 275
tupiro, 223,224
tupiru, 223
uchuba colorado, 277
uva de perro, 277
VANILLA, 68,70,77,81
anomala, 72,73,96
Griffithii var. formosana, 72, 73,96
planifolia *Andr*,, 71,91
VANILLACEAE, 70
yaje, 109–116,118–120
ZEA, 97
Mays *L.*, 1,163
mexicana *Reeves & Mang.*, 1, 163
ZEUXINE, 64

ERRATA

Page 2, line 10
for was read were

Page 85, line 32
insert a after of

Page 97, line 25
for mitotic read meiotic

Page 124, lines 4–5
for Dogbone read Dogbane

Page 124, line 19
replace period following poison with comma

Issued November 16, 1962

BOTANICAL MUSEUM LEAFLETS
HARVARD UNIVERSITY

CAMBRIDGE, MASSACHUSETTS, AUGUST 18, 1959 VOL. 19, NO. 1

THE PHYTOMER IN RELATION TO FLORAL HOMOLOGIES IN THE AMERICAN *MAYDEAE*

BY

WALTON C. GALINAT

THE structure of the inflorescences in the American *Maydeae* (maize or *Zea Mays* L., teosinte or *Zea mexicana* (Schrad.) Reeves and Mang.[1], and *Tripsacum* spp.) may be the result of developmental modifications to a repetitious pattern of organs, the "phytomer," which is basic throughout the entire plant. The parts of this pattern, as described later, have been recognized in vegetative form as an internode, a leaf, and an axillary bud (Gray, 1879 and others), and, recently (Galinat, 1956), as another organ, the prophyll.

If the phytomer and its components have a floral manifestation, then their basic homologies might be revealed by anatomical comparisons within any plant and with close relatives. Such comparisons have been successful in demonstrating the evolutionary development and homologies of certain floral structures such as carpels, compound ovaries and inferior ovaries.

We have already had some such studies in maize. The arrangement of large and small bundles has been de-

[1] This new name was proposed in 1942 and has been used regularly by its authors in a recent series in these Leaflets (Vol. 18, Nos. 7, 8, 9 and 10).

scribed in the ear (pistillate rachis) and in the tassel (staminate rachis) by Reeves (1946, 1949) and Laubengayer (1948, 1949); in the tassel alone by Kumazawa (1939); and in the culm (stalk) by Esau (1943) and others. Certain bundles in the ear have been suggested as representing those of a lateral organ (the prophyll) which is fused to the main axis or rachis (Nickerson, 1954). These previous studies are largely descriptive, interpretations being difficult because the tissues and vascularization in maize was not compared with those of its close relatives; nor was the anatomy of the rachis considered as a possible reflection of the structure of the culm. The present study attempts to examine the evolution and development of the maize plant in terms of modifications, according to function, of the organs in a single basic pattern, the phytomer.

In addition to typical maize (sweet corn inbred Purdue 39) and its relatives, teosinte (race Durango) and *Tripsacum dactyloides*, two special maize-types were included in this study. One of these is a derivative from a maize-teosinte hybrid specifically bred for a simplified version of the vascular system which could be represented in three dimensions. This breeding was done by selecting a slender, four-ranked ear with greatly accentuated cupules[2] which were free from the usual crowding and distortion. Reduced condensation to remove vertical compression between the cupules was derived from Guarany maize. Enlargement of the lateral wings of the cupules, a character associated with spikelets oriented in the same plane as that of the rachis (Galinat, 1956), was introduced from teosinte. Pairing of the spikelets, a characteristic of maize, further accentuated the cupules by spreading out the lateral wings. The other special

[2] Corneous alveoli of the maize cob immediately above the attachment point of each pair of pistillate spikelets (Sturtevant, 1899).

maize type was a heterozygous tunicate (*Tu/tu*) strain of Argentine popcorn.

The material was prepared for staining by two techniques. One of these is a somewhat unusual method similar to that suggested by Cutler and Cutler (1948) as follows:

Intact spikes (ears) were stained at the time of style emergence by placing their freshly cut bases in an aqueous solution of safranin. In a few seconds this red stain had traveled up through the vascular system and had colored all of the xylem elements. Attempts to preserve this stained material by fixing it in (3:1) absolute alcohol: glacial acetic acid and then clearing it in a cedar wood oil series were unsuccessful because the color always diffused out from the bundles and into the adjacent, highly lignified rind; but, in less lignified material, such as that of typical maize, this clearing technique was successful in revealing the vascularization of specimens stained intact. It was later discovered that, if our stained specimens were immediately dried by warm, circulating air, the red color then remained in the bundles. Free-hand, three-dimensional drawings were then made from studies of the vascular system, as revealed on the exterior of these dried and intact specimens and as reconstructed from cross-sections of the same material.

The other method used is a classical one. The material was fixed eighteen days after pollination, then dehydrated in an ethyl-alcohol series and embedded in paraffin for cross-sectioning and eventual staining. Although no difficulty was encountered with microtome sectioning in the case of the maize, the teosinte and *Tripsacum* specimens were too highly lignified at this age for easy cutting. However, a few excellent free-hand sections of only about one cell-width in thickness were obtained from the embedded material of these relatives of maize. All sections

were stained by the safranin-fast-green technique. A projection apparatus was used in making tracings from comparable slides.

Pulvini swellings from the axils of tassel branches of P39 maize were also sectioned, stained and projected in a manner similar to that used for the ears, because these small axillary protuberances appeared to represent another possible homologue of the prophyll. They were at maximum swelling when collected at the time of anthesis.

The Nature of the Phytomer

Continuity of the phytomers. The phytomer, like the cell, was once considered to be the "true individual." But now the plant as a whole is usually recognized as the individual, and the term "phytomer" is used to describe the level of organization represented by one repetition of its specialized regions or organs. The boundaries of the phytomer, and of the organs which compose it, are only approximate. Neither vascularization nor disarticulation delimit a discrete phytomer (Arber, 1934). Also such a unit is not necessarily delimited by the order of maturation, as in the classical segmentation of the phytomer used by Evans and Grover (1940) and others, because the degree and order of development of its various organs differ during vegetative and floral growth.

In order to simplify comparison of its various manifestations, we have chosen a phytomeric cycle comprising the group of organs which are adjacent to a given node or apparent node, as in the inflorescence where the nodes are usually obscure. This combination includes the leaf borne just below the node and its axillary bud with associated prophyll just above the node, as well as the adjacent internode (Plate I). The more classical delimitation of the phytomer at the nodes includes a leaf and bud

which are isolated at opposite sides and opposite ends of an internode. Our grouping is more convenient for floral comparisons, especially when the internodes are telescoped: the axillary buds are either closely associated with or fused to their subtending leaf or leaf rudiment, and the lateral organs are whorled, as in the maize ear.

Repetition of the phytomer. Control over the number of repetitions of the phytomer, as well as their individual manifestation, usually seems to follow a functional pattern which is characteristic for a certain portion of the plant. In the lower parts of the plant, all organs of the phytomer are large, photosynthetic structures (Plate I, A), while in the highly compacted inflorescences, their counterparts may be reduced or entirely obliterated (Plate I, B through F).

The typical course of repetition by the phytomer in a given area of the maize plant may be changed by unusual genetic and/or environmental conditions. In short-day maize, as in other photoperiodic plants, the number of repetitions by vegetative-type phytomers and the time of change to a floral-type of manifestation is controlled by length of day. Also the production of vegetative phytomers by axillary buds, as well as the abruptness of their ultimate shift to a floral manifestation, seem to be controlled by the corn-grass (*Cg* gene) locus. At least four other genes control the production of phytomers at specific points in the inflorescence, as follows:

The primary branches (rachids), ramosa 1, 2 (ra_1, ra_2) on chromosomes 7 and 3;

The spikelets, branched-silkless (*bd*) on chromosome 7;

The florets, polytypic (*Pt*) on chromosome 6.

Gross Structure and Manifestation of the Phytomer

Evidence of homologous relationships based on gross

structure must rely largely on a study of developmental and evolutionary variations in the manifestation of the phytomers. Discussion of such variations will orient the floral expression of the phytomer and, thereby, aid in identifying the vestiges of certain reduced parts.

Leaves. Although the leaf of the vegetative phytomer is enlarged for maximum photosynthetic activity, the floral homologue is reduced and modified according to the protective device characteristic of the species, as well as according to the order of the axis on which it is borne. At the base of the maize tassel as a whole, or sometimes at the base of each tassel branch, the subtending leaf is usually reduced (Plate I, D-1), although it may undergo all degrees of development (Galinat, 1954a). In the "central spike" of the tassel or rachis and corresponding axis of the ear, the leaf initials are usually inhibited except for a possible rudimentary leaf, the "glume cushion," at the base of the glumes. But this leaf may be well-developed in certain bamboos (Holttum, 1956), in *Coix* (where it has a protective role) and in the corn grass and teopod mutants of maize (Galinat, 1956). On the spikelet axes or rachillas, the blade-parts (laminas) of the first two leaves (glumes) are rudimentary, but in the case of the third and fourth leaves (lemmas), single genes may cause the blades to develop as awns in the "bearded" varieties of small grains, or the blades may be stimulated to complete development in proliferated spikelets.

Axillary buds and internodes. The axillary buds represent the starting points for the internodes of new axes of lesser orders. Certain variations in their derivatives (tillers, ear-shoots, tassel-branches, spikelets, florets) demonstrate the homology of the buds concerned and of the internodes of their ultimate axes. This is especially apparent in the various intergrading branches of the mutant "corn grass," which is characterized by a gradual

transition from a vegetative shoot to a reproductive one rather than the usual abrupt change (Galinat, 1954b). Spikelets may be converted into "tassel-plantlets" as an "after-effect," resulting from an insufficient number of short-days during the early floral development of short-day maize (Galinat and Naylor, 1951). The growing point of the spikelet-axis or rachilla may shift from "cutting-off" floret primordia to that of initiating spikelets as this axis becomes the rachis of an ear enclosed by husks modified from glumes and lemmas (Weatherwax, 1925). Finally, during the evolution of the maize ear, either a tassel branch or a spikelet from the tassel seems to have been modified as a tiny, sub-tassel ear which later descended to a more efficient position on the stalk, where it could increase in size (Mangelsdorf, 1958).

Prophylls. The prophyll-part of the phytomer is a two-keeled, leaf-like organ which develops at or near the axil of a lateral bud. Its two-keeled form may result from its being pressed between the branch axis and parent axis during early development (Arber, 1934). Pressure between binding leaf-sheaths and their expanding axillary buds and associated prophylls is known to be responsible for the initiation of permanent grooves in the internode of the parent axis, and, in some bamboos, this channel retains the imprint of the prophyll, even after it has been left behind by the elongation of the internode (Arber, 1934). It is apparent that the prophyll occupies the most crowded position in the phytomer, especially along the rachis, where it is either absent or highly modified and reduced. But when the position of the floral prophyll is moved away from the rachis to a less crowded position in the ultimate branches (florets), it then develops fully as the so-called "palea."

The problem then is to identify the anatomical remains of the prophyll at or near the axil of a branch within the

phytomers of the rachis. Two independent theories have been proposed for the role of the prophyll in the development of the ear and tassel of maize. Nickerson (1954) suggested that the cupule in the ear was formed by a prophyll depressed into and adnate to the rachis, except for the auricles which produce laterally as "rachis-flaps." In the tassel of maize, which lacks cupules, as well as in the paniculate rachises of other grasses, the primordial prophyll may have been contained as an axillary swelling (the pulvinus) which has become specialized to function in spreading the primary branches at the time of anthesis (Galinat, 1956). Arber (1934) has noted that the inflorescence branches of many grasses have such axillary pulvini, which expand at the time of anthesis so as to force the branches outwards; and, after anthesis, the swellings usually wilt as the branches again rise.

Internal Anatomy and Manifestation of the Phytomer

Although the homologies of certain reduced and modified organs in the floral phytomer may not be apparent externally, their basic nature may lie hidden in some part of the internal anatomy, such as that of the vascular system. An anatomical study, therefore, may help to establish the anatomical remains of the prophyll at certain of its potential positions which are occupied by other excrescences, such as the cupule in the ear and the pulvinus in the tassel.

Vascularization in maize. The homology of the floral and vegetative internodes is reflected by a close similarity in their vascular systems. Certain modifications in vascularization of the ear are caused by the reduction and compaction of lateral organs. Since vascularization in the tassel is so similar to that of the culm (Kumazawa, 1939), it will be excluded, except in regard to the pul-

vinus, from these comparative studies. The bundles of both axes tend to be of two distinct diameters which are separated into two locations (a "meristele" arrangement). Those bundles with the smallest diameters lie adjacent to the rind or lignified periphery of the axis which, in the case of the (pistillate) rachis, is repeatedly parted into the wings of numerous cupules (Plate II, fig. 1). The bundles of the large diameter are scattered throughout the pith of the culm, but, in the rachis, they are usually concentrated near the margins of the pith, where they supply the longitudinal rows of traces to the lateral spikelets, even though a few "cauline" bundles may be isolated in the center of the pith.

The diameter and position of an individual bundle is different in various parts of the plant. The larger trace-bundles, which extend horizontally from a leaf, curve downward from the leaf-node and then extend through about six internodes as they decrease in thickness and slope outward before connecting to the peripheral bundles. In the smaller trace-bundles, on the other hand, such connections occur progressively earlier in the descent, the smallest bundles remaining free for only one internode or less. As these leaf-traces descend, they supply the axillary buds along the way by means of lateral connections to a network of horizontal bud-traces slightly above each leaf node.

The glume cushions, which seem to be rudimentary leaves of the rachis, are vascularized by small bundles descending to the rind-bundles in the cupule wings below. Inasmuch as the apical end of these bundles connects with the vascular supply to the outer glumes of its axillary spikelets (Plate II, fig. 1) rather than terminating as stubs, they would appear at first to be "rind-bundles"; on the other hand, they could be rudimentary leaf-traces which have become folded inward and fused

to the glume supply. In any case, the actual elaboration of the glume cushion into a well-developed leaf under certain conditions mentioned previously seems to leave little doubt about the homology of this rudiment.

The suppression of the primary leaves along the rachis is associated with a loss of the nodal plates and differences in trace connections from the axillary buds. These traces from the binate spikelets of the rachis fan out to the nearest group of "common" bundles (Plate II, fig. 1) rather than connecting through a vascular network extending to the entire meristele, as with the axillary buds along the culm.

Nature of the bundles in the cupule wings. The evidence from vascular anatomy does not support the suggestion of Nickerson (1954) that the bundles in the cupule wings are those of a prophyll adnate to the rachis. Although the bundles located near the lateral edges of the out-folded wings of a typical cupule do have a xylem-phloem orientation opposite to that of the larger bundles within the rachis, if one follows inward along the series of bundles in such wings, the orientation of each bundle is found to twist gradually, so that the innermost ones have the same orientation as the larger bundles (Plate III, fig. 1). This twisting of bundles suggests that the cupule wings are formed in part by a gradual folding out of flaps dislocated from the rind of the rachis. Further evidence in support of this view comes from the two-ranked spikes of our teosinte-derivative of Guarany maize. The wide spacing of the cupules in this stock reveals that the rind from the barren rachis has exactly the same vascular pattern as that in the cupule wings, and that the tissue at the back of the cupule is devoid of these small bundles (Plate IV, fig. 2). It seems, therefore, that the portion of the cupule wings which includes the vascularization is derived from the rind of the rachis.

The cupule lining in relation to the pulvinus. Evidence that the wings of the cupule consist of more than just a flap of the rind comes from the experimental in-folding of these structures. When these wings are bent over into the cavity, as can be seen in the diagram of the teosinte derivative (Plate IV, fig. 2), the reconstituted axis resembles more closely the structure of the pulvinus and associated axis (fig. 1) than it does that of the culm (fig. 3). The resemblance of this wing-filled cupule to the structure of the pulvinus is revealed by close similarities in size, position and numbers of cells in the areas concerned of a sweet-corn inbred (Purdue 39). Although the total number of cells extending from the large (common) bundles outward through the center of the cupule combined with those through a folded-in wing exceeds by about thirty cells the growth which occurs between the large bundles and the epidermis of the barren rachis between the cupules (Plate III, fig. 1), it nonetheless corresponds almost exactly in number and size of cells with those which occupy the corresponding position through the pulvinus (Plate V).

Evidence of a relationship between the pulvinus and cupule lining may also be shown by a hypothetical manipulation of the pulvinus into a cupule. Starting with the pulvinus (Plate IV, fig. 1), if one visualizes a central split perpendicular to the epidermis extending inward to a point just beyond the small bundles and then diverging in both directions along a line parallel to the epidermis for the width of the pulvinus, then the flaps therein dissected will resemble in-folded wings of a cupule. By folding these wings out laterally and away from the cavity, one may produce the structure of a cupule (such as in fig. 2) in which all of the small bundles are removed to lateral wings and in which there is a layer of small cells (represented by cross-hatching) exposed over the

EXPLANATION OF THE ILLUSTRATION

PLATE I. Manifestation of the phytomer in different parts of the maize plant.

Six different phytomeric cycles	*i*	*l*	*p*	*ab*
A	internode	leaf	prophyll	axillary bud (ear)
B	rachilla segment	glume cushion	cupule-lining	binate spikelets
C	rachilla segment	lemma	palea	pistil +
D	rachis segment	leaf rudiment	pulvinus	tassel-branch
E	rachid* segment	glume cushion	rachid* scab	paired spikelets
F	rachilla segment	lemma	palea	3 anthers +

* axis of a tassel branch

Drawn by WALTON C. GALINAT

Plate I

EXPLANATION OF THE ILLUSTRATION

PLATE II. The vascular systems in the pistillate rachis of the American *Maydeae* in three-dimensional aspect. For simplicity, only that vascularization which is in the outer glume of the spikelet and in the rachis tissue adjacent to the observer is shown. Individual lines represent individual bundles except in the main bundles which are thicker and shaded when overlapped by other tissue, such as that of glumes and rind.

1. Vascularization of the maize-type rachis as represented in simplified form by a derivative from a maize-teosinte hybrid. A slight degree of twisting has been incorporated into the drawing in order to illustrate the vascular arrangement from several angles.

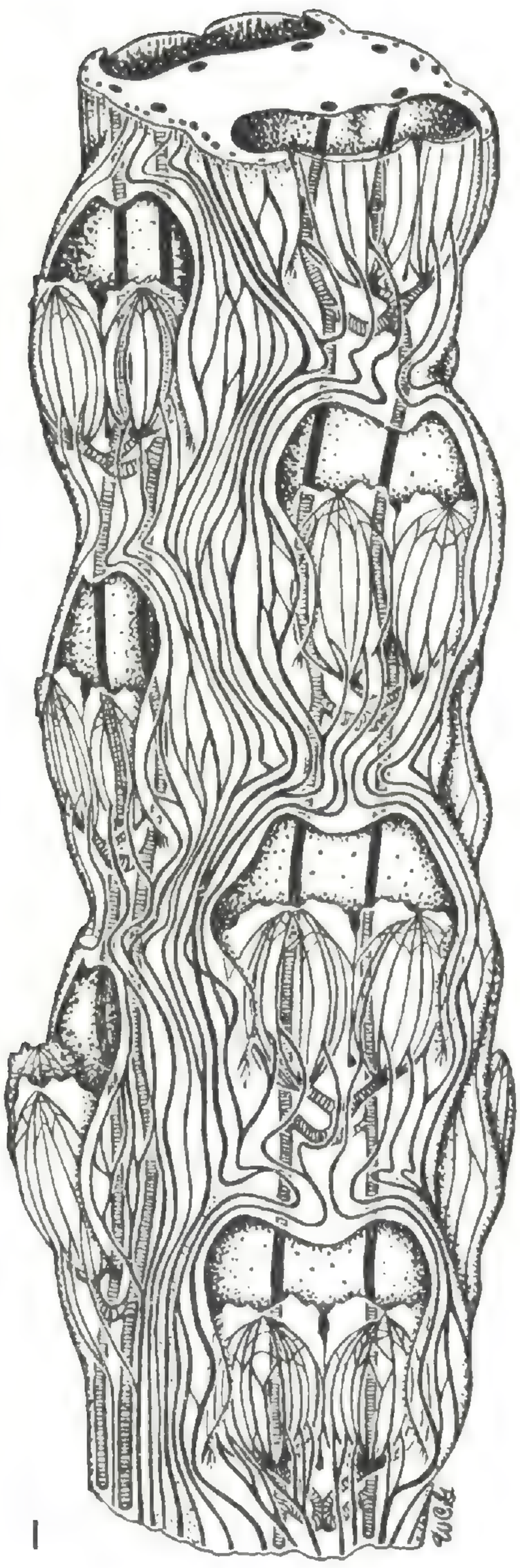
2, 3. Separate front and side views of the fruit case of Durango teosinte.

4, 5. Separate front and side views of the fruit case of *Tripsacum dactyloides*.

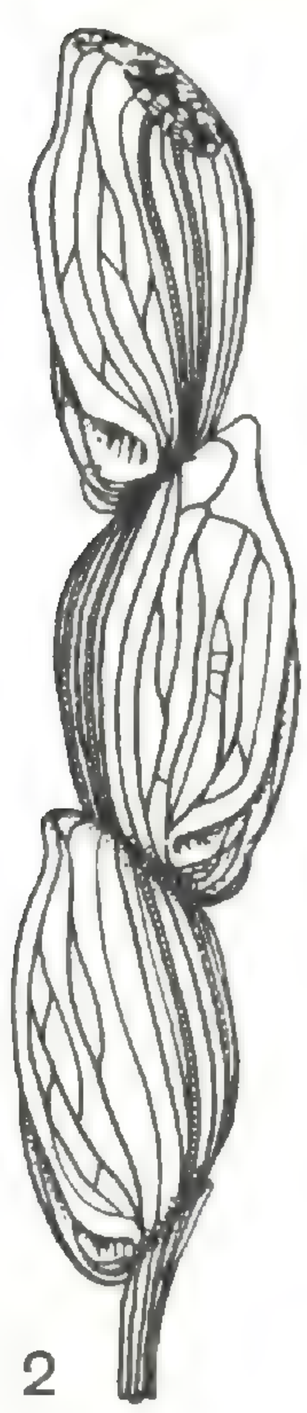
All about five times natural size.

Drawn by WALTON C. GALINAT

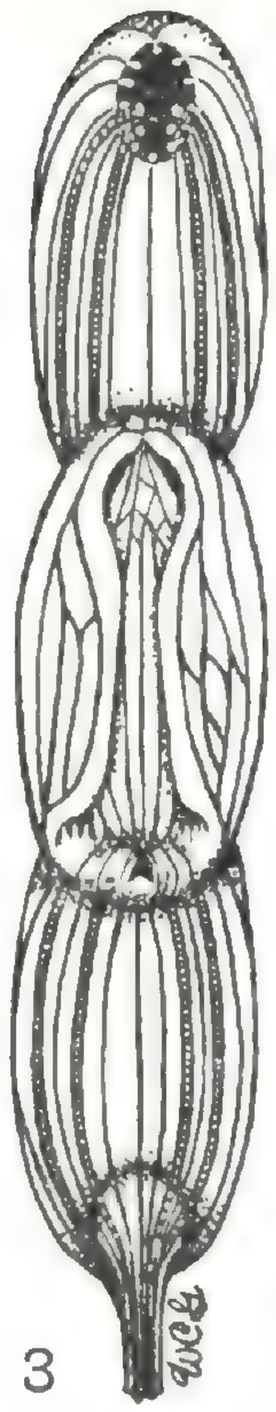
Plate II



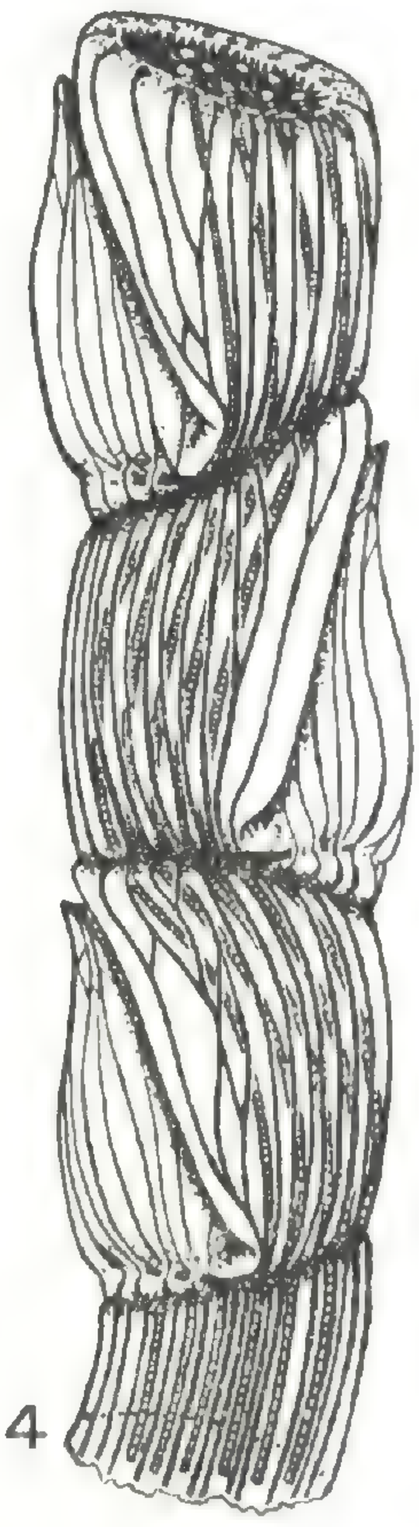
1



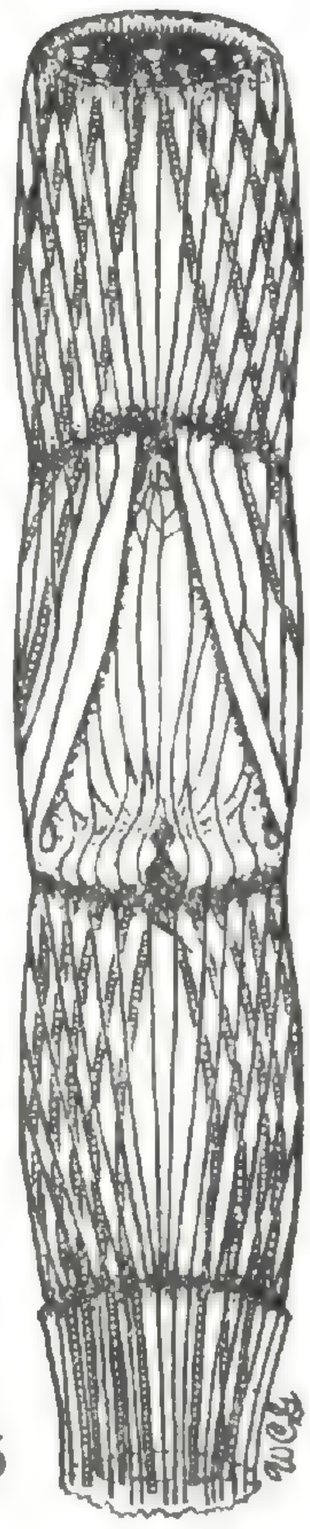
2



3



4



5

EXPLANATION OF THE ILLUSTRATION

PLATE III. Projection tracings of cross-sectional views of the cupule and rachis segment in the American *Maydeae*.

1. The cupule and associated rachis tissue of maize as represented by the sweet corn inbred Purdue 39.

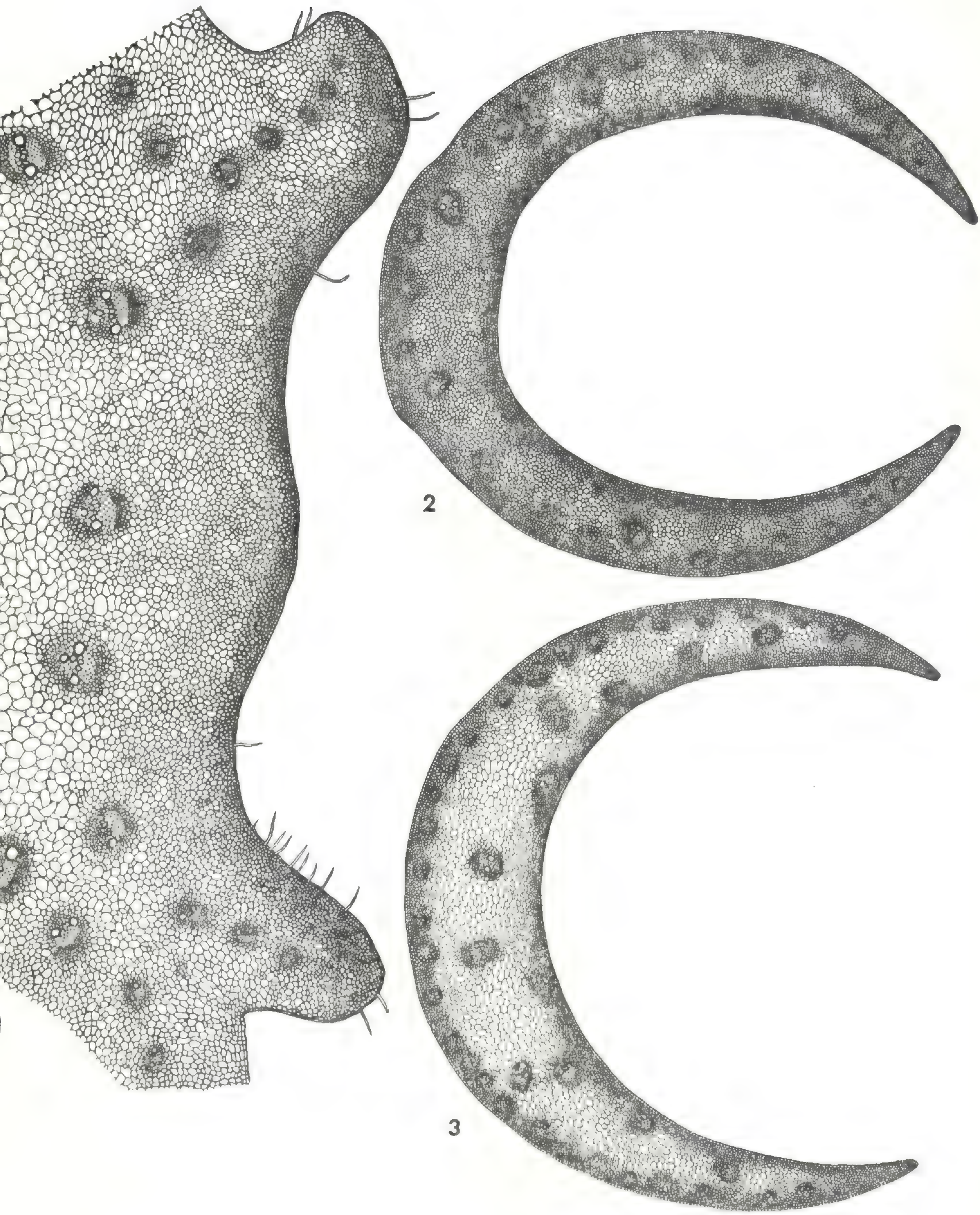
2. The rachis segment of Nobogame teosinte.

3. The rachis segment of *Tripsacum dactyloides*.

All about twenty five times natural size.

Drawn by WALTON C. GALINAT

Plate III



2

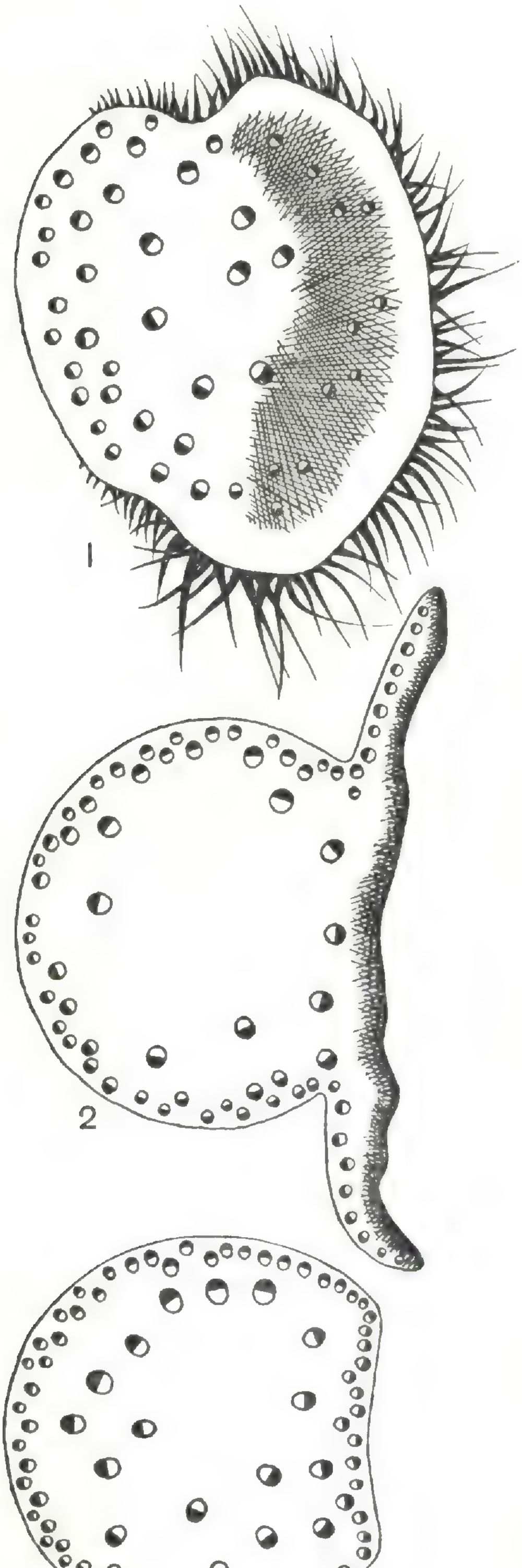
3

EXPLANATION OF THE ILLUSTRATION

PLATE IV. Diagrammatic cross-sectional representations of various axes to show structure, vascularization, pubescence, and distribution of an extremely small type of cell. The last is indicated by cross-hatching, while the phloem-region of the vascular bundles is indicated by solid black. 1, pulvinus and associated axis from a tassel branch of P39 sweet corn. 2, rachis with cupule from the distichous branch of a teosinte derivative of Guarany maize. 3, the shank associated with the spike of fig. 2. 4, the rachis of a 12-rowed ear of tunicate Argentine popcorn showing three cupules. 5, pistillate rachis of Nobogame teosinte. 6, pistillate rachis of *Tripsacum dactyloides*. All about fifteen times natural size.

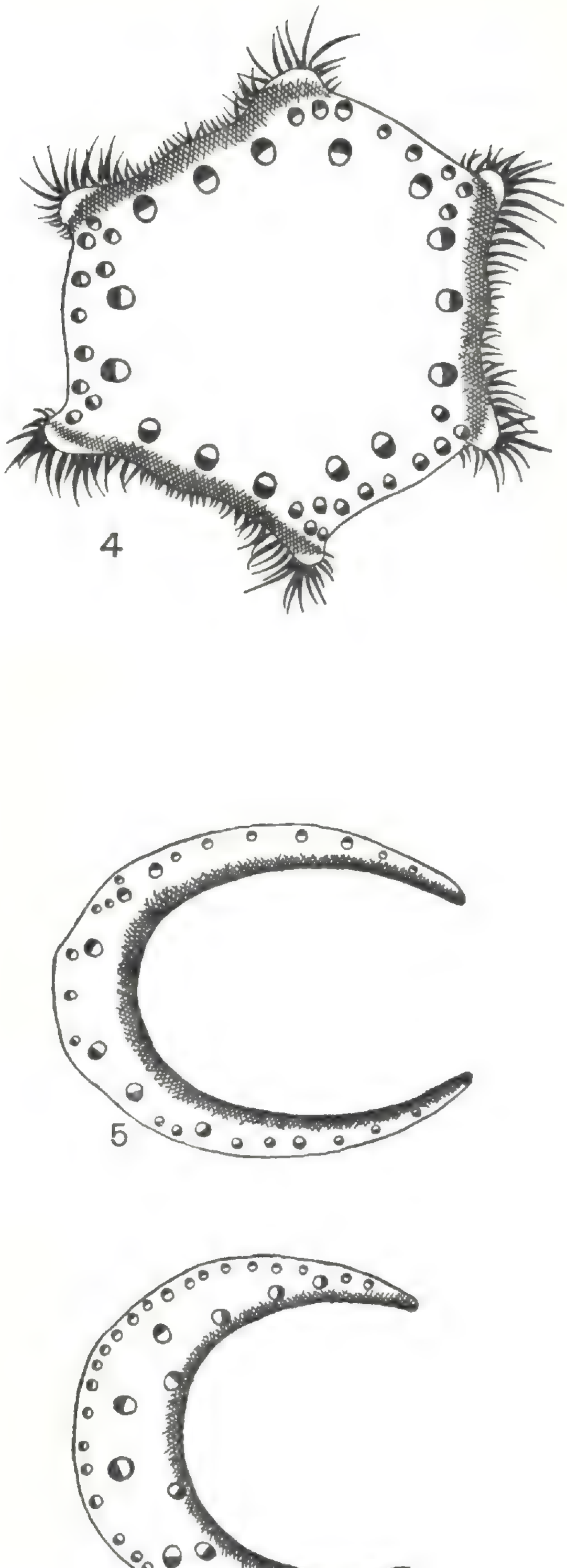
Drawn by WALTON C. GALINAT

Plate IV


1

2

3


4

5

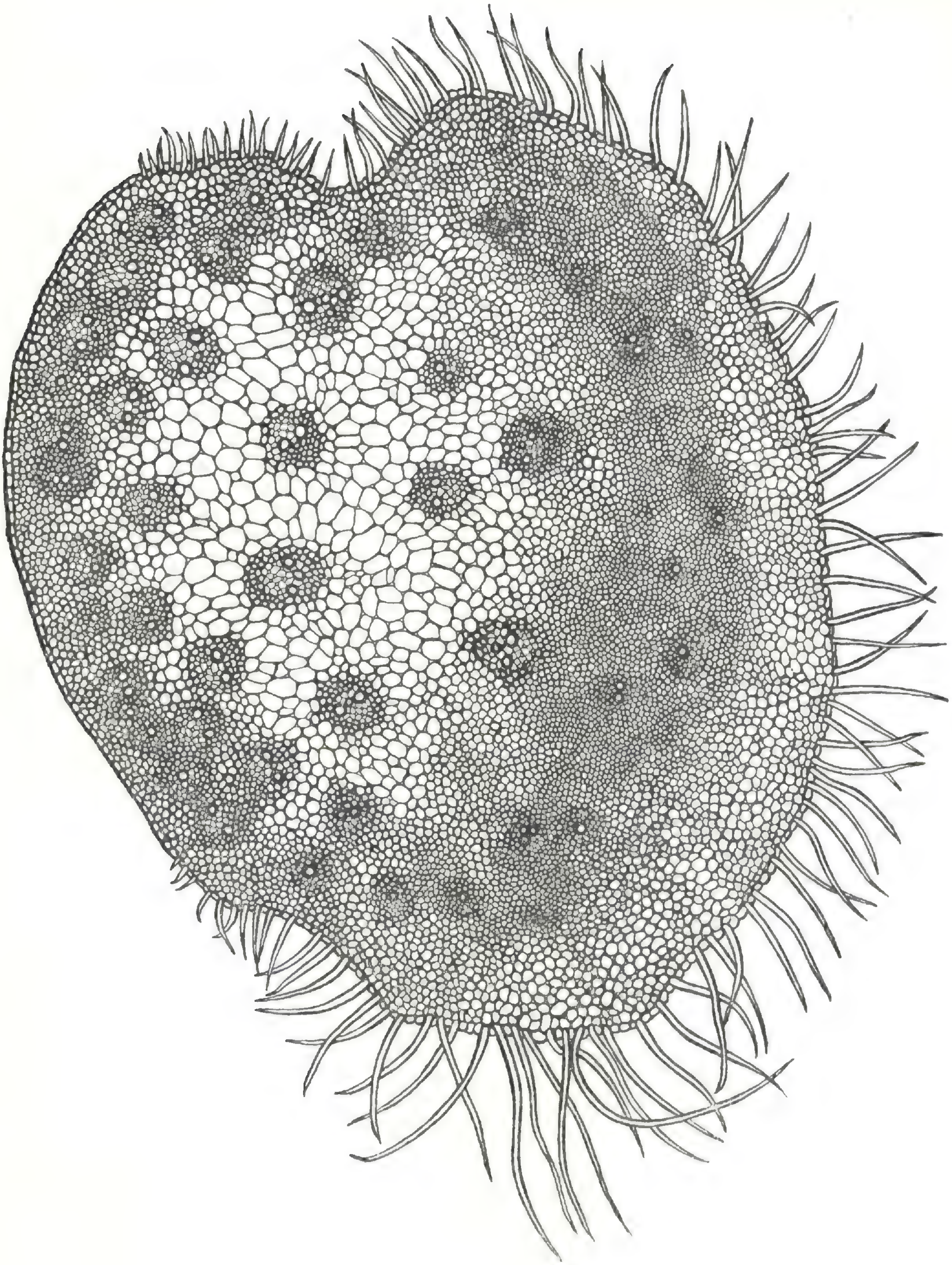
6

EXPLANATION OF THE ILLUSTRATION

PLATE V. Projection tracing of cross-sectional view of the pulvinus and associated branch from the tassel of Purdue 39 sweet corn. Note that the tissues of this mature pulvinus suggest the primordium of an organ (such as the prophyll) in that the swelling results from a proliferation of many small cells, rather than an expansion in individual cell size. About forty five times natural size.

Drawn by WALTON C. GALINAT

Plate V



surface or lining of the cavity. Such a process of cupule formation, by a hypothetical splitting of the pulvinus, serves to illustrate the similarities of the structures involved. It does not represent a plausible explanation for the origin of the cupule in terms of ontogeny, as will be noted later.

This relationship between pulvinus and cupule lining is also revealed by intergrades between these structures in tunicate (*Tu* gene) and other variants of maize. The tunicate cupules are usually shallow because of small wings and, in some cases, the "cupule" may be elevated above the adjacent rachis in such a way as to appear like a flattened pulvinus. One such type of tunicate cupule from a twelve-rowed ear of Argentine popcorn is illustrated in Plate IV, fig. 4. The hairiness and distribution of small cells in this type of cupule produce a striking resemblance to that of the pulvinus (Plate IV, fig. 1). This condition differs from the typical cupule (Plate III, fig. 1) in having all of the rind bundles crowded into corners between the cupules rather than dislocated into flaps. When tunicate cupules lack such vascularized wings, they may be "peeled" from the rachis.

Other circumstantial differences may appear during the development of the pulvinus and cupule lining. Fertilization is accompanied by a metaxenial stimulation for the deposition of lignin in the small cells of the cupule lining, while the corresponding cells of the pulvinus eventually shrink during aging of the plant. Further, the cupule or its lining is embedded into the main axis or rachis, while the axillary pulvinus usually expands along the axis of the primary branch. But the primary branches of the ear are reduced to binate spikelets which, in certain ears of tunicate maize, may be associated with pulvinus-like swellings rather than cupules. Finally, the pulvini in certain highly condensed and compressed tas-

sels, found in inbred P39, are partly formed by tissues from the main axis. Such modifications in structure are imposed by the different conditions of development in tassel and ear and do not detract from the important anatomical evidence of a close similarity between the lining of the cupule and the pulvinus.

The cupule lining and pulvinus as homologues of the prophyll. The pulvinus resembles a rudimentary prophyll in phytomeric position, in external appearance and in internal structure. The cell structure of the pulvinus suggests the primordium of an organ, such as the prophyll, in that the swelling results from a proliferation of many small cells rather than from an expansion in size of individual cells. It is rudimentary in development in being delimited by a zone of rapidly changing cells rather than by an abrupt boundary of cells such as might occur between elaborated organs which are fused (Plate V). Inasmuch as the anatomy and phytomeric position of the pulvinus is also similar to that of the cupule lining, as discussed previously, we conclude that these formations are different manifestations of the rudimentary prophyll-part of the phytomer. Therefore, it is necessary to modify our previous conception of the cupule lining as an adnate prophyll (Nickerson, 1954; Galinat, 1956) to the extent that we now believe that the cupule lining is only one of several possible manifestations of the rudimentary prophyll-part of the phytomer. Under other developmental conditions elsewhere in the plant, the tissue from this region has ultimately developed in the form of a prophyll, a pulvinus or a palea.

The role of pressure in cupule formation. The effect of pressure from constricting leaf sheaths upon floral development and floral evolution in the grasses has been recognized (Arber, 1934, and others). In maize, such pressure moulds expansion of a plastic inflorescence from the

time the plant is only a few weeks old and it continues throughout the development and maturation of the ear. Its role in cupule formation in maize and its relatives seems obvious. Here, in the position of maximum compression between two axes, the central portion of the rudimentary prophyll and associated rachis tissue seems to be depressed inward by penetration of the expanding spikelets. The resulting stresses have apparently inhibited development of the small rind bundles, while the larger bundles deeper within the rachis buckle under stress and bend inward in conformity to the depth of the depression (Plate II, fig. 1). Meanwhile, the lateral portions of the prophyllar tissue and associated rachis, which are free from pressure, bulge out as wings on either side of the penetrating spikelets. At this point in maize, lack of elongation by the internode or condensation forces the elongating spikelets to bend out and away from the cupule, finally diverging at right angles from it. This condition is in sharp contrast to that of teosinte and *Tripsacum*, as will be discussed later, where a slight elongation of the internode, as well as the rigid, sessile and solitary condition of the spikelets, leave no alternative for the spikelets but to become embedded more deeply into the rachis segment as a result of pressure from constriction.

Teosinte and Tripsacum. The homology of the cupule lining to the prophyll is more obscure in teosinte and *Tripsacum* than it is in maize, because of reductions resulting from an extreme depression of the rachis segments in these relatives of maize. The lining of the hollowed rachis segments consists of very small lignified cells similar to those which line the cupule of maize, except that they are spread out more thinly over the surface of the cavity. As with the maize cupule, these cells of the lining are smaller and more highly lignified than those of the rind. In the relatives of maize, a reduction in the

thickness of this lining is probably an effect of increased compression (Plate III, figs. 1, 2, 3).

The extreme depression of the rachis segments affects their vascularization as well. In *Tripsacum*, the larger bundles adjacent to the cupule lining are twisted into a more space-conserving position so that their longest axis lies parallel to the surface rather than in the usual perpendicular orientation, as exemplified by both large and small bundles from the opposite or convex side of the segment. In teosinte, where the effects of compression seem even more extreme, there is an actual loss of some vascularization. There are fewer strong bundles, and these lie just lateral to the dorsal position, so that they may serve equally well either of the alternate positions of spikelets from successive rachis segments (Plate III).

This increased compression in teosinte and *Tripsacum* is likewise apparent in the character of the cells in the "pith" region. In *Tripsacum*, the pith cells tend to be flattened in a direction parallel to the surface, whereas, in teosinte, the cells are restricted from expansion and, as in the glumes, small cells become lignified during kernel development (Galinat, 1957).

The physical effects of pressure in producing the above differences may be visualized by an extension of the same process used previously to manipulate (hypothetically) the pulvinus into resembling the cupule of maize. These derivations may be seen in the figures of Plate IV as follows: Having depressed the pulvinus (fig. 1) into a cupule (fig. 2), as explained previously, further concentrated pressure from single spikelets at the center of the cupule would cause the lateral wings to assume a position at right angles to that of the cupule and the cavity to sink more deeply into the pith, as the general structure and anatomical reductions come to resemble those of the rachis segments in *Tripsacum* (fig. 6) or in

teosinte (fig. 5), depending upon the degree of depression.

The extreme depression of the rachis segments in teosinte and *Tripsacum* seems to require a rigidly erect and sessile condition of solitary spikelets in combination with a thickened rachis. In the staminate rachis, the spikelets are paired, the rachis is more slender and the cupule development is weak or absent. A condition somewhat similar to that of the staminate rachis may be produced in the pistillate region by introducing the tunicate (*Tu*) gene of maize. Thus, in tunicate teosinte, as in tunicate maize, the pistillate spikelets become more pedicellate and accentuated at the expense of a more slender rachis and they are able, thereby, to bend away from the rachis sufficiently early to leave little or no depression in it. Under such conditions, the would-be cupule lining assumes many of the aspects of a flattened pulvinus (Plate IV, figs. 1, 4).

The identification of the small bundles from near the outer or convex surface of the rachis segments as rind bundles is more obvious in the relatives of maize than it is in the cupule wings of maize, because the two-ranked condition of the former, as compared to the many-ranked condition of the latter, simplifies comparison with its counterpart in the culm, which is also a two-ranked axis (Plate IV, figs. 2, 3, 5, 6). The course of these rind bundles, as well as those of the stronger inner bundles in all members of the American *Maydeae*, tends to be strictly vertical, even though in the cases of teosinte and *Tripsacum*, the spikelet positions alternate between opposite sides of the rachis. Consequently, in these relatives of maize, the small bundles from the wing area of one segment extend upwards into a dorsal position in the next segment above as they assume a position identical to those in the rind of the culm. Finally, in the third segment, some of these bundles merge with those from the

glume cushion (Plate II). The branching and fusion of small bundles is most frequent in the wing area, but such changes in the degree of vascularization may occur elsewhere in the rind. There is little doubt that these small wing bundles are actually rind bundles.

Certain extreme features of teosinte, as already noted, seem at first to be exceptions to the usually intermediate position of teosinte between its putative parents, maize and *Tripsacum*, as might be expected if teosinte be a derivative from a hybrid between these other two species (Mangelsdorf and Reeves, 1939; Reeves, 1953). These extreme features of teosinte are a more slender peduncle, a shorter spike with less pith, fewer vascular bundles, and deeper, more highly lignified cupules, as well as more numerous pistillate spikes arranged in compact clusters. But, on final analysis, all seven of these new characters seem to be a hybrid product of combining two other characters from maize and *Tripsacum*.

The derivation of these new characters might be as follows; If the erect sessile spikelets of *Tripsacum* should be combined with increased lateral compression from the tightly binding husks characteristic of the maize ear, the spikelets would become more deeply embedded in the rachis segment. Reductions in the pith, the vascular system and in cell size would follow such extreme compaction, and the smaller cells would accumulate lignin during kernel development (Plate III, fig. 2).

The "clusters" of numerous pistillate spikes in teosinte may also be explained as a recombination of two other characters: condensation in the shank (peduncle) of maize, which has lateral buds at every node, and the small, two-ranked spike of *Tripsacum*. Although the potential for the production of ears at every node along the shank occurs in most varieties of maize, it seldom develops, because the energy is concentrated into the

formation of a single large spike, the ear; but in teosinte, where the individual spikes are small, there is sufficient energy for the development of clusters of spikes.

Discussion and Summary

The structure of the entire plant of maize and its relatives results from various controlled manifestations of a basic pattern of organs, the phytomer. The parts of the phytomer have been recognized in vegetative form as an internode, a leaf, an axillary bud and a prophyll. These organs, as well as their organization in the phytomer, constitute specialized regions without exact boundaries. Nevertheless, the phytomer represents a fundamental design which occurs repetitiously throughout the entire plant. A comparison of its various manifestations is simplified, if we select a cycle comprising the group of organs which are adjacent to a given node rather than to use the classical delimitation which includes lateral organs at opposite ends of a given internode.

The reduction of parts of the phytomers which have internodes along the rachis is usually extreme. For example, the leaves which potentially subtend the spikelets are usually reduced to glume cushions or swellings at the base of the glumes, although certain genes (*Tp*, *Cg*) may stimulate their development as typical leaves. These glume cushions are vascularized by small-bundles which might be regarded as rind-bundles rather than the vascular remains of rudimentary leaves, because they connect with the vascular supply to the outer glumes rather than terminating as stubs. More information is needed concerning vascularization of swellings associated with unsuccessful attempts at leaf development.

The prophyll is another phytomeric part which is highly reduced along the rachis. In the staminate rachis at the axils of tassel branches, it assumes the functional

form of a pulvinus, an axillary swelling which has become specialized for spreading these branches at the time of anthesis. The tissues of the mature pulvinus suggest the primordium of an organ such as the prophyll, in that the swelling results from a proliferation of many small cells rather than from an expansion in size of individual cells. A study of the ontogeny of the pulvinus would be of interest in that leaf primordia (which would complete development) are usually initiated in the dermatogen or outermost layer of cells, although this condition might not necessarily apply to reduced leaves. Vascular development in the pulvinus, like that of the glume cushion, appears to be a part of the rind of the rachis.

Higher up in the staminate rachis or central spike of the tassel where the axillary buds are manifest as binate spikelets rather than as elongated branches, the rudimentary prophyll usually appears as a scab-like growth on the rachis or may be entirely reduced.

In the pistillate rachis, it is the lining of the cupules which seem to represent the prophyll. The small cells of this lining are very similar to the small cells of the pulvinus, and the physical differences in the external shape of these structures may be attributed to differences in compression during development.

The depression of the rudimentary prophyll and associated tissue is even more extreme in the relatives of maize. The result is a deeply hollowed, cupulate rachis segment which is lined with a thinner layer of "prophyllar" cells and has a distorted and reduced vascular system. Such effects are extreme in teosinte rather than intermediate between its putative parents, as might be expected if teosinte is a derivative from a hybrid between these other two species, because the extreme compression responsible is a hybrid product of combining two other characters. Accordingly, when the erect and sessile

spikelets of *Tripsacum* are subjected to increased lateral compression from tightly binding husks of maize, the spikelets then become more deeply embedded in the rachis, and various reductions in the pith, vascular system and cell size follow.

It is curious that the vascularization associated with all three of the rudiments studied—the glume cushion, the pulvinus and the cupules or hollowed rachis segments—appears to be a part of the rind of the rachis, rather than to represent vascular vestiges of their apparent homologues. But the tissues of these rudiments, as well as the effects of unusual genetic or environmental conditions, reveal their homology to organs which correspond to that of their apparent phytomeric position.

In the ultimate axes or rachillas, the parts of the phytomer become obvious. The first two phytomers of the rachilla have reduced axillary buds and produce little more than the leaves or glumes. But, in more distal phytomers, the leaves (now called lemmas) subtend a bud of sexual organs and its associated prophyll or so-called "palea."

The gross structure of the entire plant in maize and its relatives is organized upon a basic pattern of organs, the phytomer. The variations in expression which the phytomer has sought in different portions of the plant may (as Arber has suggested with respect to orders) be compared with the intrinsic beauty of a "theme with variations" as expressed in certain musical compositions. Both represent harmonious variations upon a repetitious design, and both obey the dictates of an overall plan.

Acknowledgment

During the course of the investigation and preparation of the manuscript, many helpful suggestions were made by Professor Paul C. Mangelsdorf of Harvard University.

LITERATURE CITED

Arber, Agnes, 1934. The *Gramineae*. Cambridge Univ. Press, Cambridge, England.

Cutler, H. C., and M. C. Cutler, 1948. Studies on the structure of the maize plant. Ann. Missouri Bot. Gard. 35: 301–316.

Esau, K., 1943. Ontogeny of the vascular bundle in *Zea Mays*. Hilgardia 15: 327–368.

Evans, M. W., and F. O. Grover, 1940. Developmental morphology of the growing point of the shoot and the inflorescence in grasses. Jour. Agr. Res. 61: 481–520.

Galinat, W. C., 1954a. The origin and possible evolution of sub-tassel ears in maize. Bot. Mus. Leafl. Harvard Univ. 16: 261–264.

——, 1954b. Corn grass II. Effect of the corn grass gene on the development of the maize inflorescence. Amer. Jour. Bot. 41: 803–806.

——, 1956. Evolution leading to the formation of the cupulate fruit case in the American *Maydeae*. Bot. Mus. Leafl. Harvard Univ. 17: 217–239.

——, 1957. The effects of certain genes on the outer pistillate glume of maize. Bot. Mus. Leafl. Harvard Univ. 18: 57–76.

—— and A. W. Naylor, 1951. Relationship of photoperiod to inflorescence proliferation in *Zea Mays* L. Amer. Jour. Bot. 38: 38–47.

Gray, A., 1879. Structural botany or organography on the basis of morphology. Ivison, Blakeman & Co., New York.

Holttum, R. E., 1956. The classification of bamboos. Phytomorphology 6: 73–90.

Kumazawa, M., 1939. On the vascular course in the male inflorescence of *Zea Mays*. Vascular anatomy in maize. I. Bot. Mag. Tokyo 53: 495–505.

Laubengayer, R. A., 1948. The vascular anatomy of the four-rowed ear of corn. Ann. Missouri Bot. Gard. 35: 337–340.

Laubengayer, R. A., 1949. The vascular anatomy of the eight-rowed ear and tassel of Golden Bantam sweet corn. Amer. Jour. Bot. 36: 236–244.

Mangelsdorf, P. C., 1958. Ancestor of corn. Science 28: 1313–1320.

——— and R. G. Reeves, 1939. The origin of Indian corn and its relatives. Texas Agric. Exper. Sta. Bull. 574.

Nickerson, N. H., 1954. Morphological analysis of the maize ear. Amer. Jour. Bot. 41: 87–92.

Reeves, R. G., 1946. Methods for studying the maize ear. Bot. Gaz. 107: 425.

———, 1949. Morphology of the ear and tassel of maize. Amer. Jour. Bot. 37: 697–704.

———, 1953. Comparative morphology of the American *Maydeae*. Texas Agric. Exper. Sta. Bull. 761: 1–26.

——— and P. C. Mangelsdorf, 1942. A proposed taxonomic change in the tribe *Maydeae* (family *Gramineae*). Amer. Jour. Bot. 29: 815–817.

Sturtevant, E. L., 1899. Varieties of corn. U.S. Dept. Agr. Off. Exp. Sta. Bull. 57: 108 pp.

Weatherwax, P., 1925. Anomalies in maize and its relatives—II. Many-flowered spikelets in maize. Bull. Torrey Bot. Club 52: 167–170.

BOTANICAL MUSEUM LEAFLETS
HARVARD UNIVERSITY

CAMBRIDGE, MASSACHUSETTS, JANUARY 27, 1960 VOL. 19, NO. 2

PREHISTORIC BEAN REMAINS FROM CAVES IN THE OCAMPO REGION OF TAMAULIPAS, MEXICO

BY

L. KAPLAN[1] AND R. S. MACNEISH[2]

DURING the winter of 1954, under the auspices of the Botanical Museum of Harvard University, the American Philosophical Society, the American Academy of Arts and Sciences and the National Museum of Canada, the junior author undertook an archaeological survey and excavations in Tamaulipas, Mexico. The primary purpose of this investigation was to obtain specimens and information pertaining to the origin, development and diffusion of prehistoric agriculture in the New World. One of the important foods domesticated and dispersed prehistorically was beans. This report is concerned with the bean remains found in the excavations.

Tamaulipas is the northeasternmost state of Mexico and is situated along the Gulf Coast. The southwestern portion of this state was the area surveyed. This region shows considerable range in topography and vegetation from east to west. The eastern boundary is the wide flat meandering Guajalejo River valley which has a tropical vegetation extending up from the south. West of this valley, running north and south, lies the first ridge

[1] Roosevelt University, Chicago, Illinois.
[2] National Museum of Canada, Ottawa, Canada.

of the Sierra Madre mountains. This rises to a height of 3,000 feet and is covered by a tropical rain forest with large pines on the summits. Further to the west, the valleys gradually become narrower and more canyon-like, with a more xerophytic vegetation in which maguey, cactus, mesquite and chaparral predominate. The mountains are higher (over 5,000 feet) with a thin cover of pines on their rocky summits. In this region we were fortunate enough to find three dry caves with stratified deposits representing eight cultures, associated in the main with abundant, preserved food remains (including beans).

We must first describe the archaeological findings in order to present an adequate background for an analysis of the bean remains. The sequence is based upon stratigraphy from three caves which is in part confirmed by Carbon 14 dates (see Table I). Study of the artifacts from the various occupation levels in the caves revealed similar sequential cultural complexes. Romero's Cave (Tm c 247) had sixteen occupation levels and a few artifacts below them belonging to the Infiernillo, Ocampo, Guerra, Mesa de Guaje, Palmillas, San Lorenzo and San Antonio complexes. Valenzuela's Cave (Tm c 248) contained nine stratified layers belonging to the Infiernillo, Ocampo, Flacco, San Lorenzo and San Antonio complexes, all of which had associated vegetal materials. Ojo de Agua Cave (Tm c 274) had twelve occupations and cultural remains representing the Infiernillo, Flacco, Palmillas and San Lorenzo complexes. Only the upper Palmillas level had preserved food materials. The accompanying chart Table I illustrates the dating and correlation of the stratigraphy of the three caves.

The Sequence of Cultural Phases

In briefly summarizing the cultural complexes, we

TABLE I

Cultural Phase	Estimated dates in years ago	Tm c 247 Occ. layer	Tm c 247 C. 14 date	Tm c 247 C. 14 No.	Tm c 248 Occ. layer	Tm c 248 C. 14 date	Tm c 248 C. 14 No.	Tm c 274 Occ. layer	Tm c 274 C. 14 date	Tm c 274 C. 14 No.
San Antonio	260	16			9					
		15								
	500									
San Lorenzo		14						12	520±200	M-501
	900	13			8			11		
	1100									
		12						10		
Palmillas								9		
	1800	11	1720±150	M506				8		
La Florida	2400									
		10	3440±250	M505						
Mesa de Guaje	3400	9	3650±250	M505a						
		8								
		7								
		6	4730±300	M504						
Guerra	3800	5								
					7	3945±334	c____	7		
								6		
								5		
								4		
								3		
Flacco	4300							2		
		4	4580±350	M503						
		3								
		2								
		1	5230±350	M502						
					6	5650±350	M497			
					5					
Ocampo	6000				4					
	7000									
					3					
		1a			2	8200±450	M498			
								1	8540±450	M-500
Infiernillo	9000				1					

shall emphasize what we know of the subsistence and domesticated plants utilized, with only a mention of the more diagnostic artifact types.

The people of the Infiernillo Phase were nomadic family bands of wild plant collectors who did some hunting. Nevertheless, they utilized the domesticated gourd (*Lagenaria siceraria*) and the pumpkin (*Cucurbita Pepo*). The seeds of the pumpkin, however, are extremely small and it must have been close to the hypothetical wild form if it were not actually wild. Other plants collected, which could have been domesticated, included runner beans, chili pepper and opuntia. These species, however, represented only a small portion of the diet which was composed mainly of a wide assortment of wild plants. Among the distinctive artifacts we might list Fuegian nets, loop-twine and Fuegian baskets, flake choppers, pebble smoothers, checker-woven mats with oblique corners, short incipient contracting-stemmed and small diamond-shaped projectile points, fire tongs and digging sticks. We could further enumerate a number of more general cultural traits such as several kinds of choppers, side scrapers and scraping planes, round-based points and knives, atlatl and dart fragments, twilled mats and different kinds of string with various knots in them.

Ocampo had more foodstuffs and many more artifacts. The people of this stage were semi-nomadic plant collectors who did a little hunting and who gained a small part of their sustenance from domesticated plants. Their incipient agriculture included pumpkins (*Cucurbita Pepo*), gourds (*Lagenaria siceraria*), common beans (*Phaseolus vulgaris*) of two varieties, chili peppers (*Capsicum*) and, possibly, corn. We say "possibly corn," because, although we found no cobs or kernels in the refuse, an examination of feces from these levels revealed minute particles of cobs and leaves. This discovery suggests that

small primitive or green ears had been masticated and digested, leaving no cob or kernel remains in the refuse. Opuntia and runner beans also served as food. Distinctive artifacts for this complex are Fuegian and full-turned coiled nets, three-over-three twilled baskets, twilled and plaited mats, large triangular and leaf-shaped atlatl dart points, interlocking loop-coiled baskets, gouges, antler hammers, and a wide variety of larger scrapers (planes) and choppers. There likewise occurred more general traits, such as different kinds of string and knots, mats, bone awls, wooden wedges, dart points, bifacial knives, shell beads, mortars and gourd containers.

The Flacco Phase developed directly from the Ocampo. The people of this phase were also semi-nomadic food-gatherers, but they depended more on incipient agriculture than on hunting or trapping of game. Squash, gourds, corn, chili pepper, two kinds of common beans (found in the feces), *Panicum*, amaranths, and runner beans made up apparently about twenty percent of their diet. Long contracting-stem and indented-base points, mullers and mortars, spokeshavers, Fuegian baskets, spring traps and snares, twilled baskets, simple coiled bags and elongate chisels are diagnostic traits. Though most of the heavy stone scrapers and choppers of Ocampo are not present, the more general traits continue to occur.

With the development of the semi-sedentary Guerra peoples, there occurred a fundamental shift in diet. While they still collected a vast amount of wild plants, agriculture furnished most of the energy-producing foods. The most prevalent remains are corn cobs (Bat Cave race). In addition, gourds, several varieties of pumpkin, squashes (*Cucurbita moschata*), peppers, common beans, amaranths, *Panicum* and cotton occur. The cave occupations, and also the survey, indicate the possibility that these people occupied small villages. Split-

stitch, interlocking loop, and simple stitch baskets built on a bundle foundation, small tear-drop, triangular and corner-notched dart points, rabbit sticks, leather huarches, and other objects, mullers and manos, a twined woven robe, decorated mats with woven borders, as well as a wide variety of different kinds of string, and more general artifacts give this culture a distinctive aspect.

Mesa de Guaje is very similar to the previous culture, but most of the nets and baskets have been replaced by plain weave cotton fabrics and plain black and brown pottery. Scrapers and flint tools are very rare; straight-stemmed points occur for the first time, as do manos and metates made of volcanic tufa, obsidian blades, clay disks, atlatl bunts and knotless netting. The Mesa de Guaje people definitely lived in villages. In terms of nutrition, probably more than half of their food was derived from agricultural products, the rest from wild plants. Corn is the main product and much of it shows teosinte introgression; actual grains of teosinte were found. In addition to beans (two varieties), gourds, squash, pumpkin, amaranths, peppers, cotton and sunflower seeds were present.

The next phase, called La Florida, was recognized in the survey, but did not occur in the caves. It is typical of the Late Formative of Mexico, with hand-modelled figurines, stemmed points, corner-notched points, prismatic blades, pottery bowls with tripod feet and stone-faced pyramids around plazas.

The following culture, Palmillas, represents the cultural apogee of the region. Furthermore, it represents the period of greatest diversity in agriculture. The greatest variability of pumpkins occurred at this time, as well as of gourds, warty squash (*Cucurbita moschata*) and walnut squash (*Cucurbita mixta*). A number of races of maize are present together with grains of teosinte. Three

varieties of common beans are found as well as lima and runner beans. In addition to these plants, *Manihot dulcis*, amaranth, chili, *Panicum*, sunflower, *Nicotiana* and cotton occur. In bulk, these species represent almost half the plant material found; in terms of food value, however, they represent a much larger proportion. Archaeologically, this phase is represented by a mass of material and traits. Only a bare minimum of the diagnostic artifacts will be mentioned. These include corner-notched arrow and dart points, serrated corner-notched points, engraved red, brown, and black pottery, packboards with net centers and wooden rims, complicated woven mats and cotton cloth, platform pipes and cane cigarettes, mold-made figurines, polished celts, circular pyramids and house platforms, as well as many other stone architectural features.

Though the sedentary agricultural San Lorenzo is obviously derived from Palmillas, there seems to be a short gap in the sequence and a degeneration in culture and agriculture. While all the kinds of cucurbits and beans appear, there is less variability. There are also only one or two races of corn, no teosinte, and only amaranths, peppers, cotton and tobacco. The bow and arrow, and a considerable range of arrow-point types appear; the pottery is crude — burnished, brushed and corrugated ware; the mats are decorated with colors; split-stitch bundle foundation baskets are plain; decorated cotton double-cloth occurs, and a number of small crude end-scrapers.

The San Antonio culture represents an even further degeneration, though the people of this phase seem to have been sedentary agriculturists living in "ranchos." Corn was apparently of a single race; there are only four kinds of beans. Cucurbits (*Cucurbita Pepo* and *C. moschata*), gourds, cotton and tobacco still occur. Many of

the artifacts are like those of San Lorenzo, but new point and pottery types occur as do large choppers and scrapers. Historic goods were present in some levels, and the woven twilled mats, coiled nets and cloth were much simpler.

Though the culture phases mentioned above seem to represent a unilinear development, the area, situated on the northern peripheries of Meso-America, must have had many influences at different periods from the south. It is believed that this peripheral region reflects, perhaps with some time-lag, the general sequence of agricultural practices for all of Middle America. Its geographical position just north of Meso-America indicates that it is a key area for the understanding of diffusion of agriculture into North America.

The study of our bean remains from the Tamaulipas caves, which seems to bear out these generalizations, also has considerable bearing on the solution of the problem of the origin and dispersal of prehistoric beans in the New World.

Identification of Materials

The materials examined consist primarily of desiccated and uncharred bean pods and fragments of pods. Seed remains are few and often fragmentary. Since most of the materials mentioned in this paper are pods, a brief discussion of the nature of legumes will be helpful.

In the *Leguminosae*, gross morphology of the fruit may be diagnostic in species-determination and is useful in delineating varieties of polymorphic species such as *Phaseolus vulgaris*. The legume or pod is a single carpel with two identical valves dehiscing on dorsal and ventral sutures. At the basal end, these elongate valves diverge from a pedicel and terminate at the apex in a straight or curved tip. Behavior of the pods at dehiscence is related

to their anatomy and may differ markedly in different varieties. When the fruit is mature and dry, the valves split along dorsal and ventral sutures after which they may simply separate or they may twist to varying degrees. Twisting results in dislodgment of seeds and probably aids in their dissemination. The twist of one valve is the mirror image of the other, and the twist of both is the result of a shortening of certain fiber-cells in the pod-wall.

In the production of beans which are threshed after the pods and seeds mature and dry on the plants, it is essential that the pods be of the type which do not dehisce violently with the consequent scattering of the seeds prior to threshing. The manner of dehiscence is of little importance in varieties which are customarily harvested during damp weather or which are used in the green stage.

Explosive scattering of seeds probably occurs in all wild species of the genus *Phascolus* and the loss of this characteristic must have been one of the important features of domestication and variation in beans.

The pods, and other vegetal debris examined, had been placed in separate packets, according to the site of collection, culture and occupation level. When the relative quantities of materials present in each occupation level had been estimated, tentative species-identifications were made. Many of the twisted and folded pods were extended and pressed after softening in warm water with a detergent to facilitate their identification.

Phascolus vulgaris (common beans) and *P. lunatus* (the small seeded or sieva group of lima beans) were recognized on the basis of their gross morphology. *P. coccineus* (runner beans) pod fragments were at first classified only as leguminous remains, probably of a species of *Phascolus* or a closely related genus. These remains of *P. coccineus* were later identified on the basis of the hilum

Plate VI

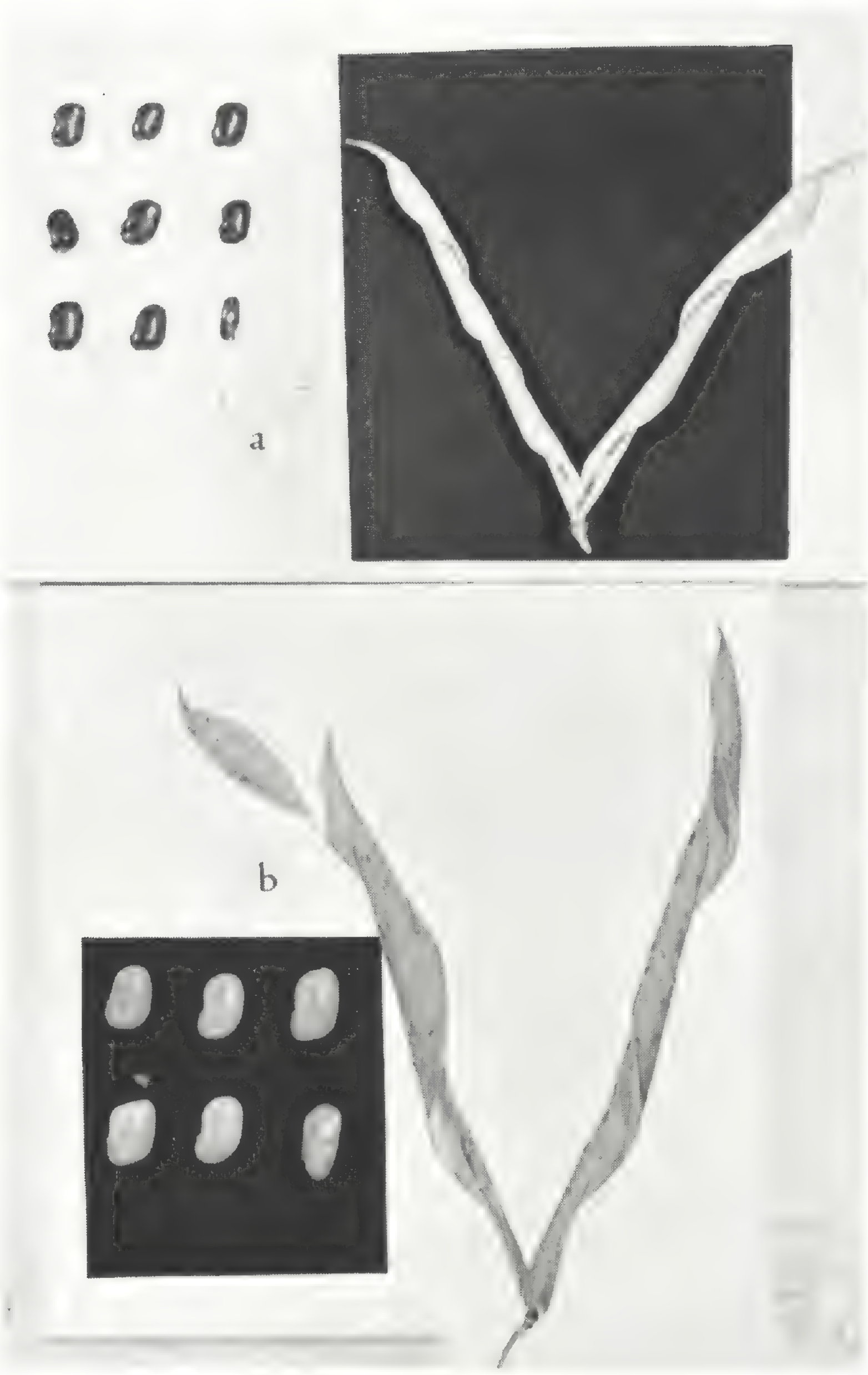


Plate VI. a, "Indigenous *Phaseolus vulgaris*." From plants grown at Lombard, Illinois by H. C. Cutler; original collection by O. W. Norvell, 14 km. north of Iguala, Guerrero. Natural size. b, "Wild *Phaseolus vulgaris*." Collected by G. F. Freytag on slopes of volcano of Colima, Jalisco. Natural size.

characteristics of a single seed coat fragment still attached to a pod valve, and the dimensions of one almost complete valve which correlated in form and texture with the previously unidentified leguminous type. Although the hilum in question is within the size range of *P. lunatus*, the separate ridges of the caruncle excluded the possibility of its being a lima bean. The hilum characteristics of this fragment are similar to those of a rather large common bean, but the dimensions and the fibrous to almost woody nature of the associated valve are similar to *P. coccineus* pods.

The possibility that this material pertained to some other species not known as a domesticate was not overlooked. Through the courtesy of Dr. Frederick G. Meyer, then at the Missouri Botanical Garden, it was possible for the senior author to examine a list of species compiled from the extensive plant collection of Dr. Meyer and Dr. R. L. Dressler. Specimens of legumes appearing in their list and which might have fruits similar to the archaeological fragments were examined in the herbaria of the Missouri Botanical Garden and the Chicago Natural History Museum. None was found to correspond to the material in question. By elimination, then, as well as by positive characteristics, the identification of *Phaseolus coccineus* was verified.

Variation in the *Phaseolus vulgaris* pods indicated their division into three types, each of which is described below. These types are to be considered as of coordinate standing with the typology presented for Southwest United States beans by Kaplan (1956). That is, in the absence of diagnostic characters which can be obtained only from the growing plants and complete herbarium specimens, the infraspecific types are without formal taxonomic standing.

Description of Types

Pod characteristics are summarized in Table III; the types discussed below have been given descriptive names and are numbered in sequence with archaeological beans described elsewhere (Kaplan, 1956).

Yellow seeded bush, C 31. The bush habit is indicated by remains of two plants with fragmentary fibrous root systems diverging from the bases of stems bearing fruiting branches. The curved pedicels are 0.8–1.5 cm. long borne in pairs on 5–6 cm. peduncles. The pods would have been borne at 15 to 20 cm. above the soil surface and appear to be fewer than 10 per plant, although this could be highly variable. This variety was probably harvested by pulling up the entire plant, since many of the pods have remained attached to stem sections. In contemporary Mexico, bush beans are frequently harvested in this manner; the bundles of dried plants are stored in or near the habitation and threshed by beating on a mat as opportunity or need arises. The yellow to yellow-tan color of the rare seed coat fragments associated with the pods represents possibly a change in hue from cream.

This group includes thin-walled variants probably picked when young. Thick-walled variants are more common, particularly in the San Antonio phase; 20 of 26 fragments in one San Antonio packet are thick-walled. It is not possible to say whether this is a genetic variation or the result of growing conditions. Lesions which appear to be anthracnose (*Colletotrichum Lindemuthianum*) injuries are found occasionally on all types but are abundant on the thick-walled variants.

Black seeded bush, C32. The pods are moderately curved with thin and relatively non-fibrous walls. In the immature condition, the fruits of this type might have been useful as snap beans; displacement of the intersti-

TABLE II

DISTRIBUTION OF BEAN REMAINS

Culture	Tentative age years ago	*P. coccineus* valves	*P. vulgaris* valves				*P. lunatus* valves	Total in each culture
			C31	C32	C33	C33a		
San Antonio	200–500	1	40		35			76
San Lorenzo Occupations 13,14,15,16	500–900	21	296	45	111	4	3	480
Palmillas	1100–1800	11	206		14		1	232
Mesa de Guaje	2400–3400		16		3			19
Guerra	3400–3800		1					1
Flacco	3800–4300	13						13
Ocampo (Portales)	4300–6000	4	5		1			10
Infiernillo	7500–9000	14						14

tial parenchyma tissue, however, shows that the seeds were mature when harvested. A single pod of this type was found containing three small black seeds (Table III). The non-twining shoots on which pods have persisted indicate this to be a bush variety probably harvested in a manner similar to that suggested for the previous type. In contrast to all other beans described here, the valves of almost all of the "black seeded bush" type are joined at the base and attached to the pedicel.

Long pod, C 33. The pods are curved but show little variation in breadth from base to tip, that is, there is little tapering; nor is there constriction of the dry pods between the seed positions. Most of these valves are dark reddish brown in color and have a cartilaginous rather than fibrous texture when wet. An occasional pod is encountered with the pedicel and peduncle still joined; these are approximately 1 and 3 cm. long respectively. None of the fruiting branches is attached to a main stem, suggesting that "long pod" is vining and that harvesting involved the pulling of individual pods as is the common contemporary practice with pole beans. No seeds have been found attached to the pods. A few fibrous-walled variants of C 33 (C 33a in Tables II and III) are present with more seeds than the type and are correspondingly larger.

Discussion

Runner beans

Of greatest interest in this group of legumes is the occurrence of remains of *Phaseolus coccineus*, constituting the first definite archaeological record of this species (Kaplan, 1956). In contemporary agriculture, these beans are grown mainly in the highlands of Chiapas and the Valley of Mexico. From the Federal District to Querétaro, they are frequent, and further north they are

TABLE III

SPECIES AND VARIETAL CHARACTERISTICS

SPECIES & TYPE	POD CHARACTERISTICS					SEEDS			
	length cm.	dorso-ventral width cm.	twist of valves	no. seeds per pod	tip	length cm.	width cm.	thickness cm.	color
P. vulgaris									
C31	7–9	0.8–1.2	slight	3–6	short-straight	fragments only	—	—	yellow to yellow tan
C32	6–7.5	0.7–1.1	slight or none	5	straight to down-curved	9–1.0	0.6	0.4	black
C33	11–13.5	1	moderate	7	few intact fragile	—	—	—	—
C33a	13–15	1–1.5	moderate	8	few intact fragile	—	—	—	—
P. coccineus	greater than 11	1.5 or more	tight	—	none intact probably short and stout	—	—	—	dark, probably purple
P. lunatus	about 12	3	slight	—	none intact				

Plate VII

Plate VII. a, *Phaseolus coccineus*. Pod fragments from the Infiernillo and Ocampo cultures. Natural size. b, *Phaseolus vulgaris* (yellow seeded bush C31), three pod valves. From Palmillas culture. Natural size. c, *Phaseolus vulgaris* (long pod C33), pod fragments. Slightly less than one half natural size. From San Lorenzo Culture.

found only occasionally in Mexico and in the southwestern United States, where at least two varieties are cultivated by the Hopi. Runner bean use by the Hopi is almost certainly an historic introduction in view of their absence from archaeological sites thought to be associated with Hopi prehistory.

In July 1957, Kaplan briefly visited Ciudad Ocampo, below the Sierras in which the caves are situated, taking with him pods of the excavated *Phaseolus coccineus* and seeds of purple variegated and self-colored, white, modern runner beans. During the Sunday market, residents of Ocampo and others from villages higher up in the Sierras were shown the samples and asked to identify them. No one recognized the seeds or pods as belonging to either wild or cultivated plants with which they were familiar. It is safe to conclude that *P. coccineus* is not now utilized in the area in which the excavations were made.

The archaeological runner bean pods, notwithstanding their morphological similarities to modern types, differ from them in certain microscopic features. Some of these differences are quantitative and are related to cell-wall thickness and fiber-cell size. Furthermore, the archaeological pods are more tightly twisted than are those of modern cultivated varieties. Most striking is the abundance of sclerids or stone cells in the archaeological material as contrasted with their absence in modern runner bean pods. Although the reduction of sclerids in the domestication of fleshy fruits is of obvious adaptive value, it would not constitute a selective factor in the domestication of beans. Even if the pods were used in the green state, it is doubtful that the appearance of more edible varieties with fewer stone cells ever occurred as the result of human intervention. Since these stone cells affect qualities of pods which would be used in the immature state, any selection for their reduction would have re-

quired the application of rather advanced concepts of plant breeding probably not at the disposal of pre-Columbian peoples in the New, or, for that matter, in the Old World. It may be that the deposition of lignin to form stone cells is related to more general physiological processes which were subject to selective influences.

There is no apparent dissimilarity between early and later *Phascolus coccincus* pods in this site. There are no pods which could be considered as intermediate in reduction of hard texture and fiber between the early Tamaulipas material and modern varieties.

There are, then, remains of *Phaseolus coccineus* pods, anatomically more primitive than modern types, in inhabited sites and corresponding at later occupation levels (see introduction and Table II) with definite evidences of agriculture. Several closely related problems remain to be solved. These are: the absence of *P. coccineus* from late Flacco to the beginning of Palmillas (Table II); the failure of the species to persist into historic times in this region; and its status as a domestic or wild plant during the periods of cave occupation.

The disappearance of runner bean use in Tamaulipas resulted probably from the effect of climatic change on plant distribution. Preliminary studies (MacNeish, in conversation) indicate that this region has passed through at least two warm climatic cycles. The earliest of these was presumably warm and moist, as its duration was marked by the presence of *Manihot* from late Flacco to about the beginning of Palmillas (see Table II). Runner bean remains are absent during this thermal period of more than 2000 years, although they are present both before and after. This absence cannot be explained by the prevalence of poor conditions for vegetal preservation in the caves, since cucurbit materials are abundant from this period (Whitaker, *et al*, 1957).

The reappearance of *Phaseolus coccineus* after the beginning of Palmillas suggests strongly the response of a wild rather than cultivated plant. We would hardly expect a cultigen absent for 2000 years to be reestablished merely with the return of favorable climatic conditions. Reintroduction is a possibility, but from where? The southwestern United States could not have been a source for reasons already noted. Plant migration from regions south of Tamaulipas would have been highly unlikely, since conditions there would have been even less favorable for the survival of a cultivated plant with cool temperature requirements. An indigenous plant, on the other hand, might have formed relic communities in protected locations becoming more generally distributed and available for human use at the end of the thermal period. A second thermal period might well have been the cause of the extinction of *P. coccineus* from this part of its natural range.

The hypothesis that *Phaseolus coccineus* may have been a wild rather than a cultivated plant in Tamaulipas is supported by the extreme age of the remains and their occurrence long before the practices of ceramic cooking and agriculture, and by the apparent lack of selection for pod characteristics found in modern cultivated varieties. If runner beans were present, but not domesticated, in Tamaulipas in spite of their being included in the gathered plant complex prior to and during agricultural times, another problem arises. Why would so useful a food plant be neglected as a domesticate in Tamaulipas but be brought into cultivation in Chiapas? The answer is to be found probably in the reaction of *P. coccineus* to the differing photoperiods in these widely separated areas of its range.

Allard and Zaumeyer (1944) studied the reaction of various leguminous plants to day-length. A daily expo-

sure to less than 13 hours of daylight resulted in an appreciable delay in flowering date of *Phascolus coccineus* which was accompanied by tuberization of the root system. Longer day-lengths brought about earlier flowering, and tuberization did not occur. Chiapas, at about 16° North latitude with days of less than 13 hours of light during the growing season, corresponds to the delayed flowering-tuberized root situation, while Tamaulipas at about 23° North latitude has photoperiods of more than 13 hours during most of the growing season.

In the highlands of Chiapas, the fleshy roots of runner beans are eaten by Tzeltal Indians (fieldwork, 1957). If this be a retention of an early practice (as suggested by Edgar Anderson in conversation), then it is possible that domestication of runner beans was based upon root as well as seed use. Such a practice could not have occurred in Tamaulipas since tuberization does not occur because of the long-day, short-night condition.

The early presence of *Phaseolus coccineus* remains makes it advisable to examine any wild populations of bean species which are otherwise known only as cultivars. Kaplan has collected *P. coccineus* in a variety of situations, including pine and oak forests and deep *barrancas*, in Chiapas. None of these sites has been under cultivation in the memory of local inhabitants, but the strong tendency of this species toward perenniality leaves open the possibility that these plants are relics of cultivation. However, Ephraim Hernandez X. has stated (in conversation) that *P. coccineus*, and other closely related species, which are not escaped or relic cultivars do occur in Chiapas. Probably the most important related species is *Phaseolus polyanthus* Greenman which also seems to be planted with *P. coccineus* and reaches the markets with beans of this latter species. Oliver W. Norvell has noted such market mixtures in seed collections in the herbarium

of the Chicago Natural History Museum (herbarium accession numbers 981251 and 1119897). The caruncle ridges of this species are less distinctly separated than those of *P. coccineus*.

Concerning the distribution of *Phascolus polyanthus*, Piper (1926) says only that the type specimen is from near Jalapa, Vera Cruz, where it was collected on a railway embankment (Greenman, 1907). Piper further notes that specimens which may be from wild *P. coccineus* plants have been collected near Puebla, Puebla; Monte Escobedo, Zacatecas; Saltillo, Coahuila; Tacuba, Mexico; San Juan Capistrano, Jalisco; Tumbalá, Chiapas; and Frajanco Santa Rosa, Guatemala. As yet, there is, unfortunately, not sufficient information concerning affinities and barriers between putative wild *P. coccineus* and wild possibly interbreeding species, and domesticated *P. coccineus* to draw any conclusions concerning systematic relationships.

Common beans

Types of *Phascolus vulgaris* not generally distinguishable from modern cultivated varieties appear in abundance beginning with the Mesa de Guaje level, at about the same time that intensive agriculture and fired ceramic wares were introduced. Bean remains in non-agricultural, pre-pottery Ocampo and Guerra cultures are limited in number. This situation is similar to that in the Southwest, where in the Mogollon and Basketmaker–Pueblo regions the increase in bean remains is correlated with the introduction of pottery (Kaplan, 1956).

Common beans, appearing for the first time in the Ocampo culture, join the already established *Cucurbita Pepo* (Whitaker, *et al.*, 1957). Both of these plants antedate the appearance of corn. This is the only area in which common beans have been shown to occur prior to

corn and the early bean types persist into more recent archaeological times.

The presence of these bean types in early pre-pottery times followed by an expansion of their use with the introduction of pottery agrees with the hypothesis presented (Kaplan, 1956) to account for the remarkable constancy of bean types over long time spans in the Southwest. This hypothesis postulates that beans entered as domesticates very early, were sparingly cultivated until the use of pottery began and then the same, long established, well adapted varieties came into more general use.

Collections of specimens determined as wild *P. vulgaris* have been made by G. F. Freytag, O. W. Norvell, A. Burkart and others. The only published account of wild and cultivar affinities which goes beyond morphological comparison is that of Burkart and Brücher (1953). A wild *Phaseolus* species collected in Central and South America, and studied by these authors, has proven to interbreed with *P. vulgaris* and although the floral morphology is similar, differences in seeds, pods and leaves exist. As a result of their studies, revisions in the nomenclature of *P. vulgaris* L. were proposed by Burkart and Brücher (1953).

The various collections identified as wild *P. vulgaris* have all been vining types with seeds smaller than those encountered in most cultivated varieties. It seems that the determinate growth habit as well as increase in seed size and reduction of pod-shattering have been established under domestication.

Sieva beans

Small seeded limas, or sieva beans, were introduced late and never attained much importance. Their paucity here substantiates other evidence indicating that these

beans entered the southwestern United States from the west. Sievas appear in the Verde Valley and at Point of Pines, but not in the more easterly Mogollon and Basket-maker–Pueblo areas. With the study of additional remains in the future some relationship between southeastern United States and northeastern Mexico sievas may be shown.

Tepary beans

The absence of tepary beans (*P. acutifolius* var. *latifolius* Freeman) supports our present knowledge of their pre-Columbian and historic distribution. Bukasov (1930) and others have indicated a western distribution for contemporary tepary cultivation, while Carter (1945) has shown a spread of tepary cultivation from south-central Arizona to the north and east in late pre-Spanish times.

Summary

1. A total of 845 bean pod fragments from three archaeological cave sites in Tamaulipas, Mexico, were studied and identified. These remains consist of: *Phascolus vulgaris* (3 domesticated types), *P.coccineus* (one nondomesticated type), *P. lunatus* (one domesticated type).

2. These beans are considered to be distinct from those occurring in prehistoric time in the southwestern United States.

3. It is thought that *P. coccineus*, although gathered as a useful wild plant, was not domesticated in this region because of non-tuberization of the roots under the photoperiod conditions of Tamaulipas.

4. *P. vulgaris* remains first appear with preagricultural materials 4300–6000 years ago and are the oldest com-

mon beans yet reported. They antedate corn but are later than squash in these sites. *P. coccineus* remains, the earliest of which are dated 7500–9000 years ago, constitute the only archaeological runner beans on record. *P. lunatus* remains are few and were present 500–1800 years ago.

BIBLIOGRAPHY

Allard, H. A. and W. J. Zaumeyer. 1944. Responses of beans (*Phaseolus*) and other legumes to length of day. U. S. Dept. Agric. Tech. Bull. 867: 1–24.

Bukasov, S. M. 1930. The cultivated plants of Mexico, Guatemala and Colombia. Bull. Appl. Bot. Gen. Pl. Breed., Suppl. 47: 151–176. Leningrad. (Mss. translated from the Russian by H. J. Kidd, Ann. Mo. Bot. Gard. 41: 271–299. 1954.)

Burkart, Arturo and H. Brücher. 1953. *Phaseolus aborigineus* Burkart, die mutmassliche andine Stammform der Kulturbohne. Der Züchter 23 (3): 65–72.

Carter, George F. 1945. Plant geography and culture history in the American Southwest. Viking Fund Publ. Anthrop. 5: 1–140.

Greenman, J. M. 1907. New or Noteworthy Spermatophytes from Mexico, Central America and the West Indies. Field Col. Mus. Bot. Ser. 2: 247–287.

Kaplan, Lawrence. 1956. The cultivated beans of the prehistoric Southwest. Ann. Mo. Bot. Gard. 43: 189–251.

Piper, C. V. 1926. Studies of American Phaseolinae. Smithson. Inst., U.S. Nat. Mus. Contr. U.S. Nat. Herb. 22: 663–701.

Whitaker, T. W., H. C. Cutler and R. S. MacNeish. 1957. Cucurbit materials from three caves near Ocampo, Tamaulipas. Amer. Antiq. 22: 352–358

BOTANICAL MUSEUM LEAFLETS
HARVARD UNIVERSITY

CAMBRIDGE, MASSACHUSETTS, MAY 19, 1960 VOL. 19, NO. 3

ON THE ORIGIN OF THE ORCHIDACEAE[1]

BY

LESLIE A. GARAY

INTRODUCTION

To discourse on the origin of the Orchid family, which represents the culmination of one of the evolutionary lines of the Monocotyledons, is a rather formidable task. Its existing members display such a high degree of complexity of organization in their structures that the primitive characters or simple elements, which might have shed light on ancestral origins, are either lost or well masked. When we take into consideration that the Orchid family, comprising at present some 30,000 species distributed in 800 genera, is devoid of paleobotanical documentation, save *Protorchis monorchis* Massal. from the Eocene of Monte Bolca, it is impossible to explain or even state the manner in which the various evolutionary forces have acted upon the primordial organism that served as the prototype for modern species. In addition to these difficulties, information on the anatomy, embryology, genetics, cytology, fertilization, ecology, etc., of today's species is too fragmentary to give us a reliable and coherent picture.

In spite of these deficiencies, I shall attempt to present an outline of the Orchid family and its origin, as I

[1] This paper will be read on May 31, 1960 during the 3rd World Orchid Conference in London, England.

understand it, from an interpretation of the evidence now available, as well as to point out the gaps where intensive research is required for further clarification. It is my hope that this effort may stimulate the students of evolution to turn some of their attention to this intricate and perplexing group of plants.

The problem of the origin and phylogeny of various plant groups and families has occupied the minds and interest of a number of outstanding botanists from Linnaeus to our time. All have recognized that in nature a system prevails within which everything seems to follow a pattern of progressive differentiation from simplicity to complexity. While Linnaeus' sexual system can hardly be associated with progressive differentiation, the systems of Bentham and Hooker or of Engler and Prantl, to mention but two, in essence convey this idea. However, progressive differentiation in the light of our modern species-concept assumes an entirely different role and meaning from that which was understood and employed by the earlier workers. A glance at any of the proposed "natural" systems is sufficient to make us recognize that they are based on a continuous modification along a straight line of descent. We are informed today, however, that species could also have been derived simultaneously or consecutively from a common ancestor or from the fusion of one or more common ancestors. Progressive differentiation in the light of these latter principles assumes an entirely new and far reaching significance.

If we wish to understand the origin or phylogeny of any group, regardless of its taxonomic status (genus, subfamily, family, etc.), we must first understand the basic unit: THE SPECIES. A lengthy discussion about the nature of species does not, however, lie within the scope of this paper, and I must assume that the reader is fully acquainted with the subject. It is sufficient, there-

fore, if we merely state that the species represents a dynamic, adaptive peak in evolution. Any taxonomic group above this level, in order to express a meaningful expansion, must represent further dynamic macro-units or enlarged adaptive peaks (which are the results of the coaction and coaptation of the basic units), because if these higher units are merely categories of convenience (as most of them are today) they will hinder rather than broaden our perspective and comprehension of the evolutionary makeup of our object of study.

We have to keep constantly in mind that living species are scanty representations of all the possible modifications and combinations that may have occurred in nature, although those types which have been eliminated by selective pressures still contributed to the formation of present species. Therefore, when we study a group of plants, we find that its basic units (i.e. species) are connected by a series of trends which are radiating in various directions, forming a reticulate pattern. In visualizing this reticulate pattern in a three-dimensional perspective, we find that the connective trends progressively decrease as we advance towards higher levels, but that this decrease never terminates in complete elimination.

Such a dynamic and 3-dimensional structure (vaguely resembling the molecular structure of a crystal) cannot be projected into a 2-dimensional perspective without destroying, or at best distorting, its salient features.

All of us, from time to time, have felt and recognized the presence of such a system, but our conventional mind with its categorizing instinct continuously interferes with and obscures our vision. I wish to make it clear that I fully recognize the necessity of categories of convenience, but I strongly object when these categories of convenience are employed as the basis of a so-called "natural" system; and this is what has happened in the case of the Orchid family

Keeping constantly in mind the dynamic structure of nature, I shall attempt to examine the Orchid family and its origin against this background.

Floral diagrams and basic groups

The Orchid family is an extremely heterogeneous unit with respect to its external and internal composition. The vast array of types of modified structures, many of which combine simultaneously characters of both a primitive and advanced nature, are, however, tied together by a few definite characteristics: 1, the inferior ovary; 2, the production of a large number of seeds without endosperm; and 3, the various degrees of fusion between the style and stamens.

Notwithstanding the large number of species in the family, it is possible to outline and express the arrangement of floral parts by means of three or four basic floral diagrams (Plate VIII). From an inspection of these floral diagrams, it is evident that orchid flowers are built on a trimerous pattern and that they are merely modifications of the liliaceous type. The essential deviation from the liliaceous pattern is to be seen in the staminal circles. In the first diagram (Pl. VIII, fig. 1), which may equally serve for *Ornithogalum* of the *Liliaceae* or *Hypoxis* of the *Hypoxidaceae* (*Amarillidaceae* sens. lat.), both staminal circles are fertile and fully developed, i.e., all six anthers are functional. In the *Orchidaceae* (Pl. VIII, figs. 2–4) the anthers opposite the lateral sepals and the median petal are completely suppressed (with the exception of *Satyrium*, about which more will be said later). The reduction in number of fertile anthers is always paralleled by a fusion of the stamens and of the stamens with the style. Developmental and anatomical investigations with respect to the origin of these fertile circles indicate that the existing species must have evolved along at least two different lines from an already modified ancestral type,

1 HYPOXIS

2 NEUWIEDIA

3 SELENIPEDIUM
APOSTASIA

4 NEOTTIOIDEAE
OPHRYDOIDEAE
KEROSPHAEROIDEAE

5 SATYRIUM

because each of these lines, although still sharing detectable characters, displays an unequal rate of differentiation. These functional circles, or the number of functional anthers present in these circles, are still employed today to characterize the two major subdivisions of the family.

In *Neuwiedia* (Pl. VIII, fig. 2), there are three fertile anthers, one dorsal and two ventral. This is the only genus in the family *Orchidaceae* where fertile anthers are present simultaneously in both staminal circles. In this respect *Neuwiedia*, one of the three genera of the *Apostasioideae*, is perhaps the most primitive orchid: the other two genera, *Apostasia* and *Adactylus* are merely modifications of the *Neuwiedia*-pattern. In *Apostasia* (Pl. VIII, fig. 3), we observe a transformation of the dorsal anther into a staminode, while in *Adactylus* a further suppression completely eliminates this structure. *Apostasioideae* are set apart from the rest of the orchids by an additional series of correlated characteristics which will be discussed in further paragraphs.

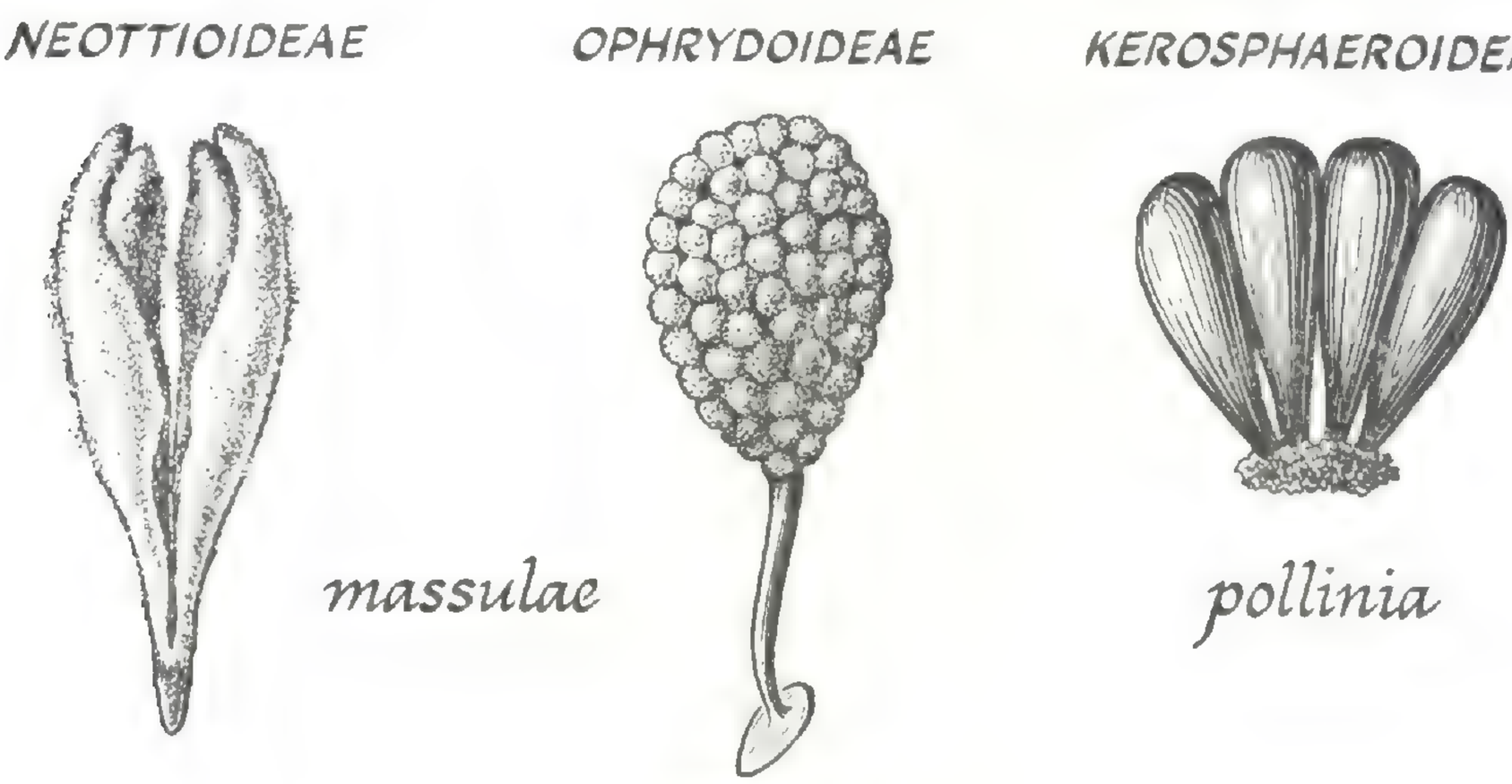
Although the floral diagram of *Apostasia* is identical with *Selenipedium* (Pl. VIII, fig. 3) of the group *Cypripedioideae*, this identity is restricted to diagrammatical representation. The vegetative appearance, as well as the floral morphology in both of these groups, is very dissimilar. In *Apostasioideae*, the filaments of the anthers are usually still present and recognizable; while in *Cypripedioideae* these structures are completely fused with the style. Furthermore, in *Cypripedioideae*, the shape of the staminode and the median petal exhibit a major deviation from *Apostasioideae*, to such an extent that these two groups can hardly be interpreted as representing two subsequent stages of one evolutionary trend.

The discontinuity between *Neuwiedia* and the monandrous orchids is even greater. The floral diagram (Pl. VIII, fig. 4) brings into focus a single criterion only: the

suppression of a different staminal circle. This suppression seemingly conveys the idea that *Neuwiedia* gave rise simultaneously to both *Cypripedioideae* and to the monandrous orchids. However, the sum total of characteristics which make up the monandrous orchids suggests that during the course of evolution there were other lines besides that of *Neuwiedia* which fed into the complex. Although the general pattern of the monandrous orchids (which include 90% of the known species) can be expressed by a single diagram, the group itself is composed of three distinct units, depending on the manner and degree by which the individual pollen grains adhere to each other to form the pollinia. These three groups are: *Neottioideae*, *Ophrydoideae* and *Kerosphaeroideae*.

In *Neottioideae* and *Ophrydoideae* (text fig. 1) the pollen grains are of a soft consistency and cohere into massulae in a relatively loose manner; in the former unit they easily separate into a fine powdery mass (sectile pollinia), while in the latter they form large granules (granular pollinia). In *Kerosphaeroideae* the cohesion of the individual grains is so compact that the pollinium may be broken only through the exertion of considerable force.

The presence of pollinia is characteristic of the three units of monandrous orchids only. In the *Apostasioideae*



Text fig. 1

and *Cypripedioideae*, no pollinia are formed; the anthers contain single pollen grains either dry or embedded in a viscid secretion respectively.

Endomorphic and Exomorphic features

Vascularization. The distribution of vascular bundles in the stem and inflorescence-axis of orchids exhibits the same more or less scattered arrangement as is generally observable in the vegetative axis of other Monocotyledons. The bundles are enclosed within a sclerenchyma-like ring of perivascular fibers, either in a circular manner (similar to the primitive *Aristolochia* type in Dicotyledons) or in a scattered pattern. A preliminary investigation indicates that the circular pattern is always associated with other primitive characters. Those species which exhibit this characteristic have a more or less well developed horizontal rhizome (e.g. *Apostasia*, *Cypripedium*, *Zeuxine*, etc.). Nevertheless, more information is needed before the significance of this association may be fully and definitely evaluated.

In the vascular supply of the flower, the bundles which enter the floral axis vary in number, and this variation is correlated with the primitive or advanced stage of the group. Swamy reports the number of vascular bundles in the *Cypripedioideae* as six; in the *Neottioideae* and *Ophrydoideae* and the less specialized members of the *Kerosphaeroideae* three; while in the advanced types of the *Kerosphaeroideae* there is a further reduction in number to two. Our investigation of the *Apostasioideae* reveals six vascular bundles, as is the case in the *Cypripedioideae*.

In *Apostasioideae* and *Cypripedioideae*, the six bundles constitute the main traces of the ovary without further differentiation. In both of these groups, there is an additional seventh bundle which gives rise to the midrib of the bract.

In the remaining groups (*Neottioideae*, *Ophrydoideae* and *Kerosphaeroideae*) the entering three or two bundles already differentiate in the pedicel to supply the ovary with its six main traces. The pattern by which these six traces of the ovary proliferate in passing to the floral and sex organs is uniform throughout the family. The three dorsal bundles of the ovary enter directly into the three sepals, with a trace leading from each of them to the gynostemium; an additional branch deviates from the main bundle which supports the dorsal sepal to the anther of the outer whorl. The three ventral bundles of the ovary enter directly into the petals, the two lateral ones giving rise to a trace which supports the anthers in the inner whorl. The main trace of the bract is also derived from one of the three incoming bundles.

The presence of six undifferentiated bundles in the *Apostasioideae* and *Cypripedioideae*, as contrasted with three or two in the monandrous orchids, is a further indication of the relative primitiveness of these two groups.

Placentation. The ovary in the Orchid family is syncarpous, either three- or one-carpellate (Plate IX). The three-carpellate condition, i.e. with axile placentation, is present in all species and genera of the *Apostasioideae*, in *Selenipedium* and *Phragmipedium* of the *Cypripedioideae* and in a few genera of the *Neottioideae* (*Lecanorchis*, *Eriaxis*, etc.). The remaining genera of the *Cypripedioideae* and the monandrous orchids exhibit a monocarpellate ovary, i.e. the placentae are parietal in origin.

It is generally accepted that axile placentation is a more primitive condition than parietal, and its occurrence in the Orchid family is limited to groups of respectively primitive status.

Our knowledge with regard to the manner of transition from axile placentation to the parietal type is very meager. Two seemingly aberrant types, i.e. *Phragmi-*

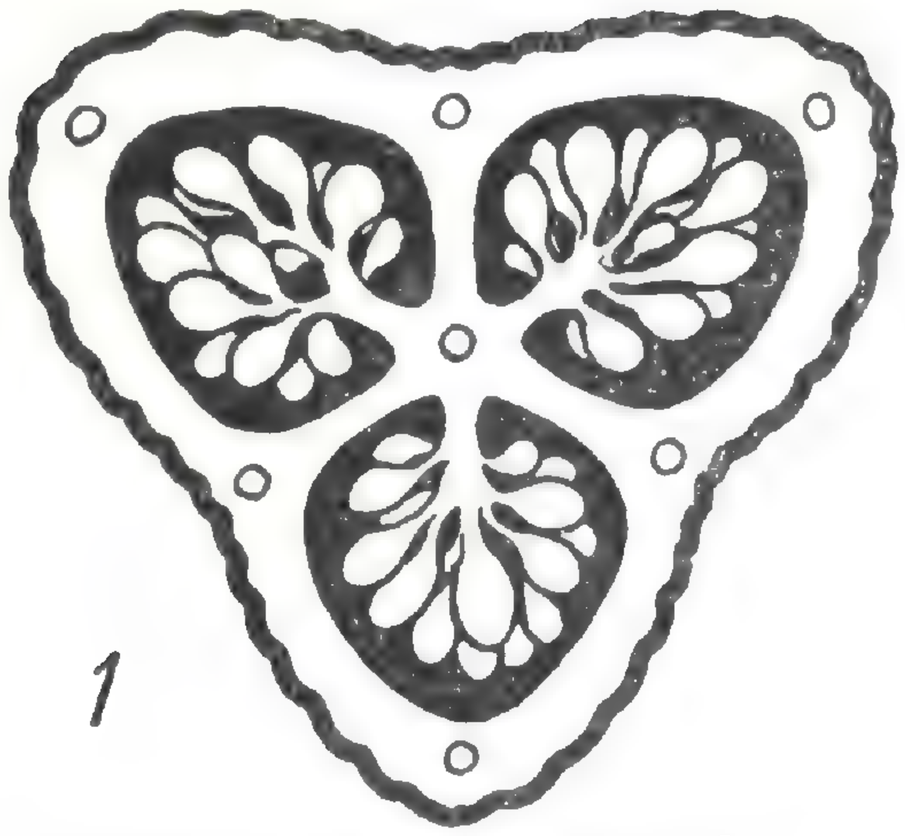
pedium longifolium (*Cypripedioideae*) (Pl. IX, fig. 3) and *Lecanorchis javanica* (*Neottioideae*) (Pl. IX, fig. 4), however, may possibly represent independent steps in the reduction process. Theoretically, the placentae in *Phragmipedium longifolium* are parietal in origin because each of the two placental lamellae, although situated in adjacent locules, are vascularized by a common strand (note the connecting dotted arrow). The placentation itself is intermediate between the axile and parietal positions. In *Lecanorchis javanica*, we find another type of modification of axile placentation. The septa are broken down into separate placental lamellae, and the torus is completely eliminated. The individual lamellae facing the adjacent ventral bundles are united by the margin, thus leaving a Y-shaped empty cavity in the center of the ovary, and the ovules are borne in two rows at the point of junction of the lamellae.

These intermediary steps suggest that the reduction from a tricarpellate to a monocarpellate condition might have come about by a longitudinal division of the septa which eliminated the torus, followed by a gradual shortening of the lamellae (*Limodorum abortivum*, Pl. IX, fig. 5), until merely traces are found along the inner wall (*Cephalanthera alba*, Pl. IX, fig. 6).

Embryogeny. No other plant family exhibits such an inconsistent embryogeny as the *Orchidaceae*. Only the first and second cell generations of the zygote are consistent; the subsequent divisions apparently take place in a random manner.

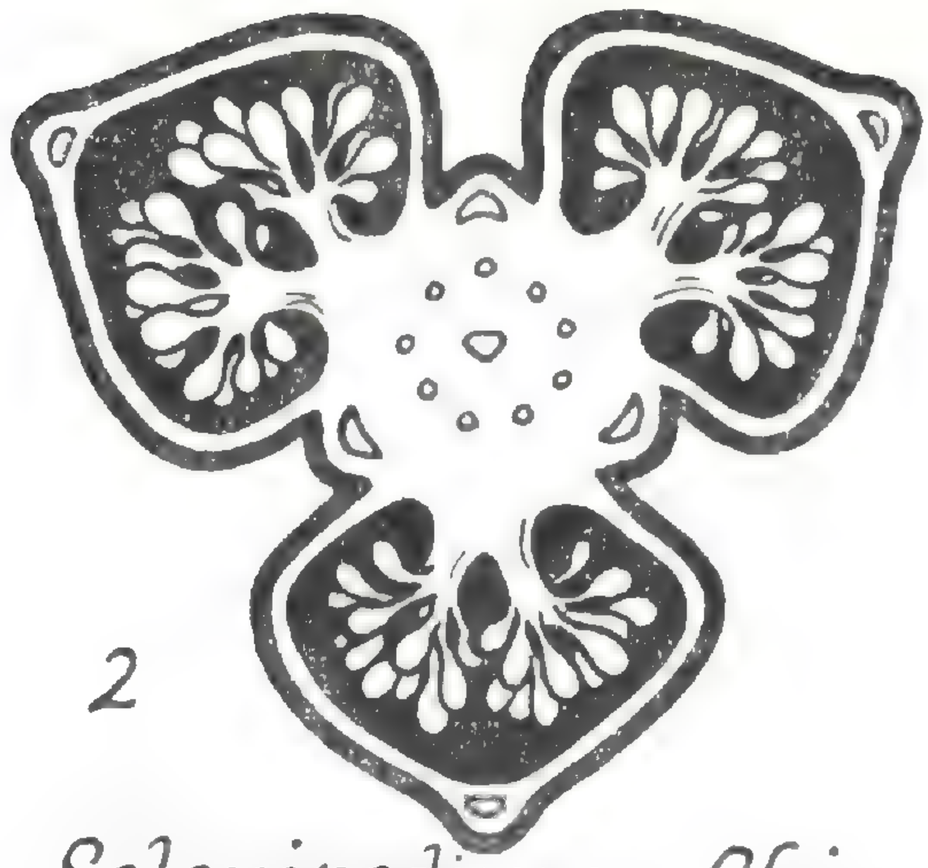
In the first cell generation (Pl. X, fig. 1), the zygote divides into a basal and terminal cell. During the second cell generation, the basal cell differentiates into a suspensor initial cell and middle cell, while the terminal cell divides by a vertical wall. From this step onward, the further divisions are without any definite sequence, but

Plate IX



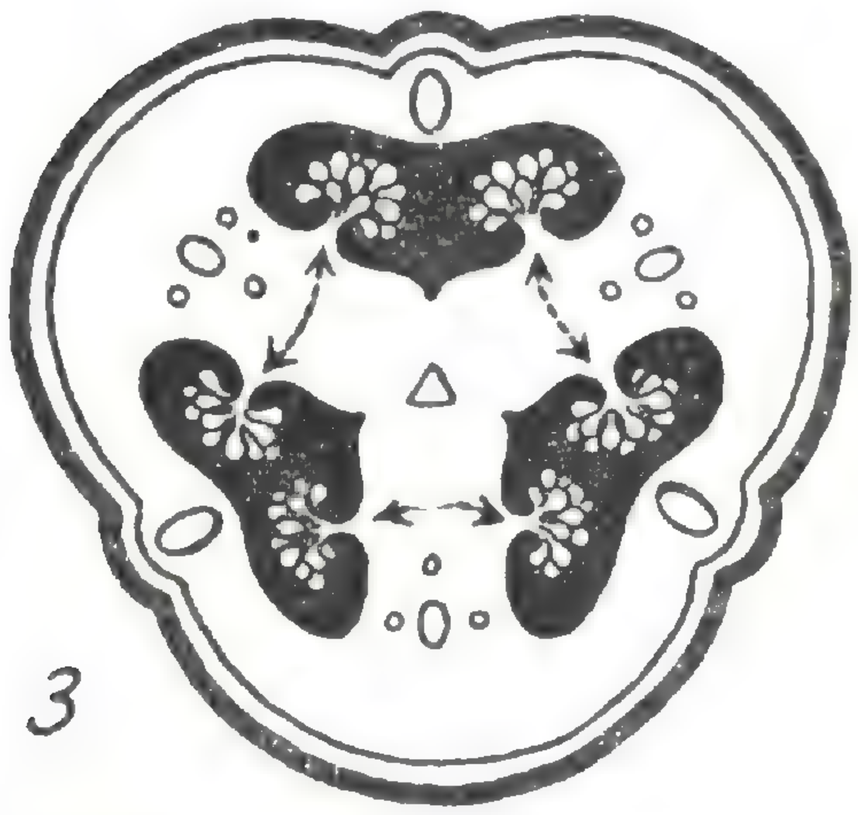
1

Apostasia nuda



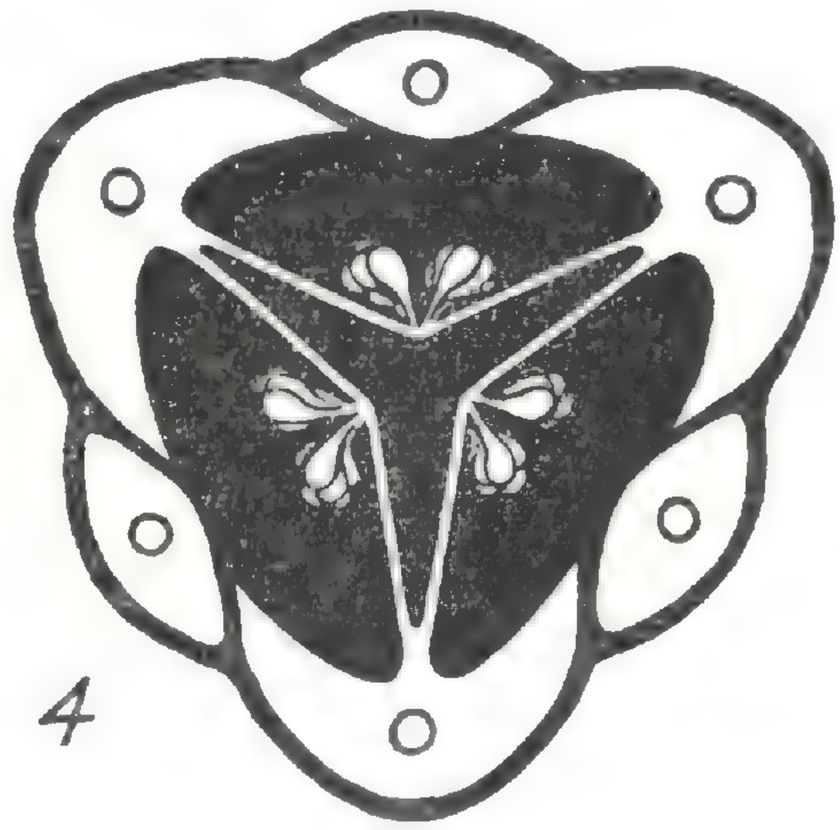
2

Selenipedium Chica



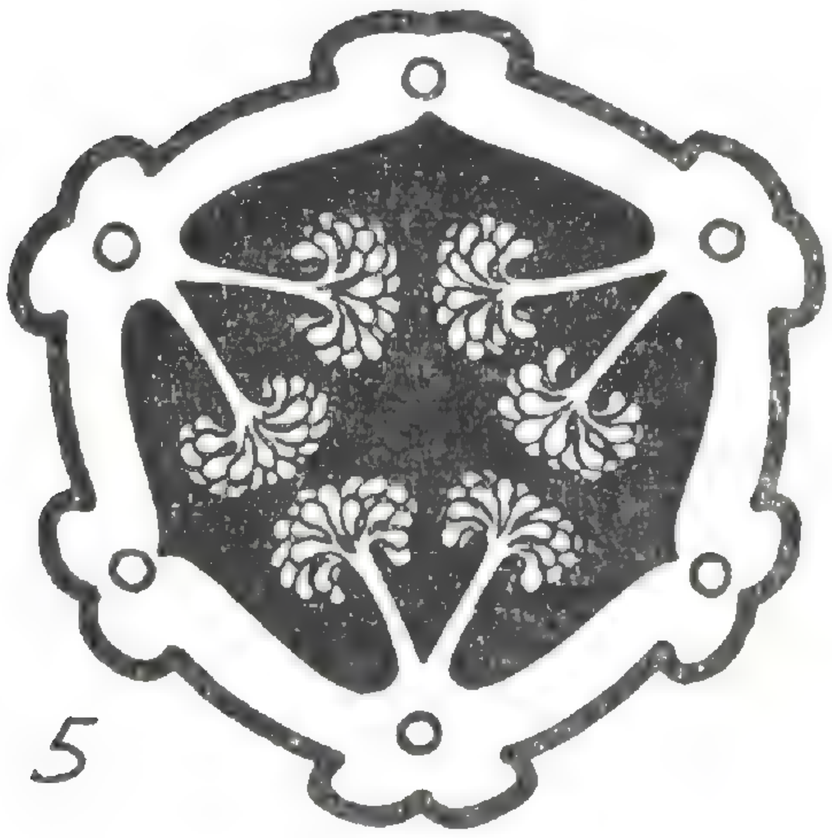
3

Phragmipedium longifolium



4

Lecanorchis javanica



5

Limodorum abortivum

6

Cephalanthera alba

the development may be oriented in two directions: 1. (Pl. X, fig. 1A) all cells including the suspensor initial cell enter into the formation of the embryo, and the mature embryo is suspensorless; 2. (Pl. X, fig. 1B) the suspensor initial cell appears as a distinct structure, either simple or modified.

The suspensorless type of embryo is primitive and is to be found in *Cypripedium* of the *Cypripedioideae* and some members of the *Neottioideae* (*Spiranthes*, *Listera*, *Neottia*, etc.), while those with a suspensor are distributed among the rest of the groups. Swamy, after having studied the embryogeny of a number of species, recognized five different types of suspensors (Pl. X, fig. 2): TYPE I, with a single-celled suspensor, occurring in *Cypripedioideae* (*Paphiopedilum*) and also in the *Neottioideae* (*Vanilla*, *Epipactis*, *Goodyera*, etc.): TYPE II, which is unique in the family in developing a haustorium, is limited, so far as is known, to the *Ophrydoideae*. TYPES III to V are found in various representatives of the *Kerosphaeroideae*.

There is a striking parallelism or correlation between the various types of suspensors and the relatively primitive or advanced stage of the main groups of the family.

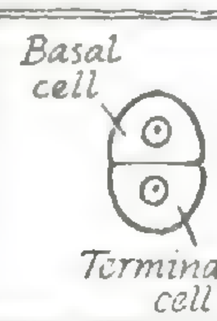
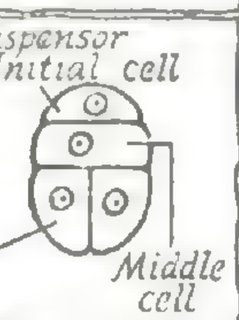
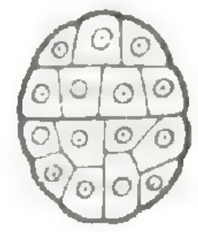
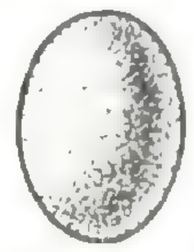
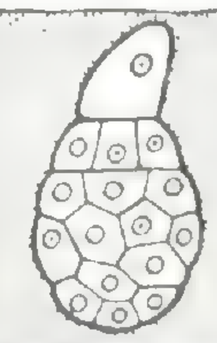
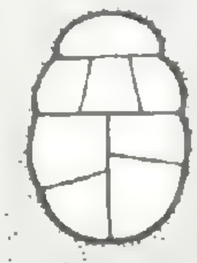
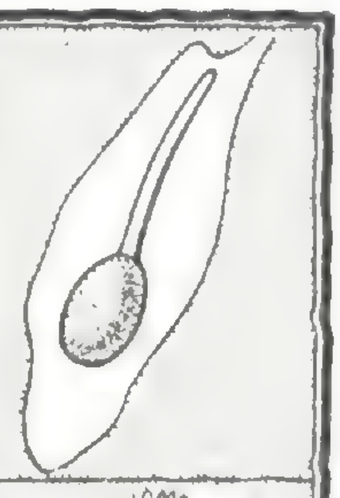
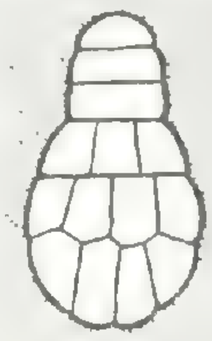
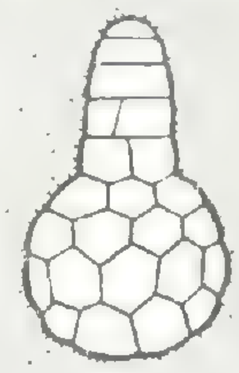
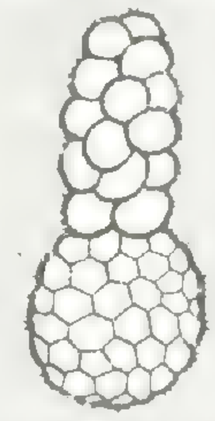
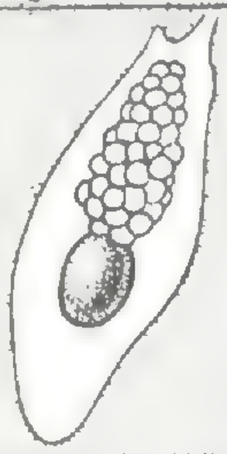
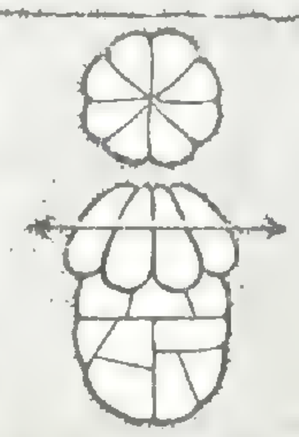
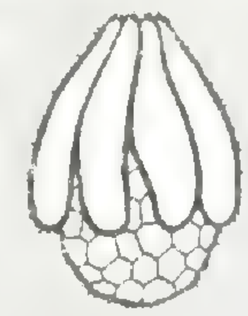
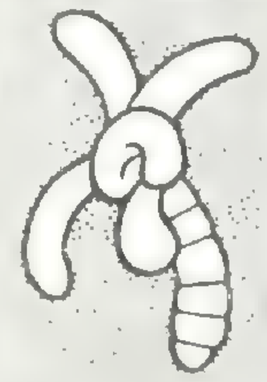
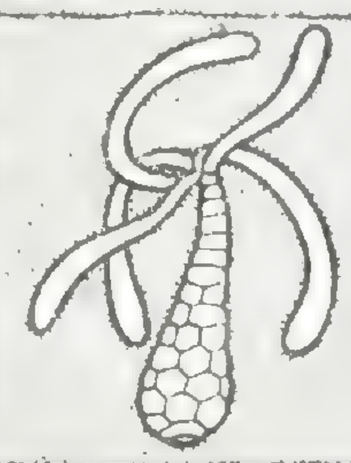
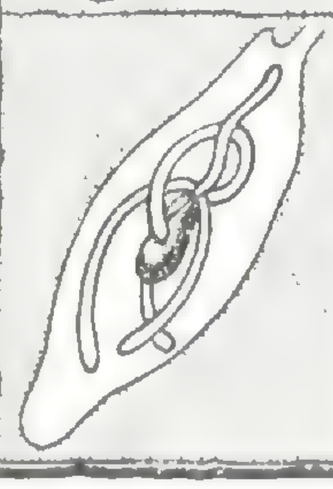
The mature embryo is an ovoid mass of cells without any definite differentiation of the tissues; thus, there is no endosperm in orchids. With respect to the method by which the undifferentiated mass of cells becomes organized into the several organs of the embryo, no information is available as yet. In a few instances, endosperm development has been reported, but in all of these this development is not consistent. Whenever it occurs, the tissue is of the nuclear type. This rare and casual occurrence is noted in the *Cypripedioideae* and *Neottioideae*.

Seeds. The mature embryo is enclosed in a loose, air-filled, reticulate testa which is characteristic of the *Micro-*

Plate X

1

2

	Zygote	1st Cell Generation	2nd Cell Generation	(Intermediate step)	Adult Organization
GROUP A					
GROUP B					
TYPE I					
TYPE II					
TYPE III					
TYPE IV					
TYPE V					

spermae (Pl. XI, A). At maturity the cells of the outermost layer of the integument lose their protoplast, and the seed coat becomes transparent. This type of seed is observable in every genus of the family, except in *Apostasia*, *Adactylus*, *Selenipedium* and *Vanilla* (Pl. XI, B). In these four genera, all layers of the outer integument and most of the inner integument enter into the formation of the seed coat which tightly surrounds the embryo; the testa becomes highly sclerotic, opaque and sculptured.

It is rather remarkable that the presence of a primitive type of seed in *Apostasioideae*, *Cypripedioideae* and *Neottioideae* corresponds to the respective status of these groups.[1]

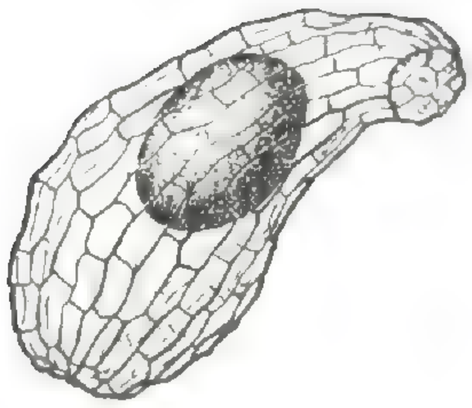
Gynostemium. One of the most distinct features of the *Orchidaceae* is the fusion of the stamens and style into a central organ, the column. This structure has generally been interpreted as an extension of the floral axis, thus being axial in origin. Recent studies, however, have shown it to be only an appendicular structure, since the morphological apex of the flower does not extend to the apex of the gynostemium, but only to the level of insertion of the perianth; the ovary contains all traces of the floral whorls and the gynostemium of the reproductive whorls.

Even today there is a constant debate about the meaning and application of the terms "column" or "gynostemium." The group *Apostasioideae*, from time to time, has been kept apart from the *Orchidaceae* as a distinct

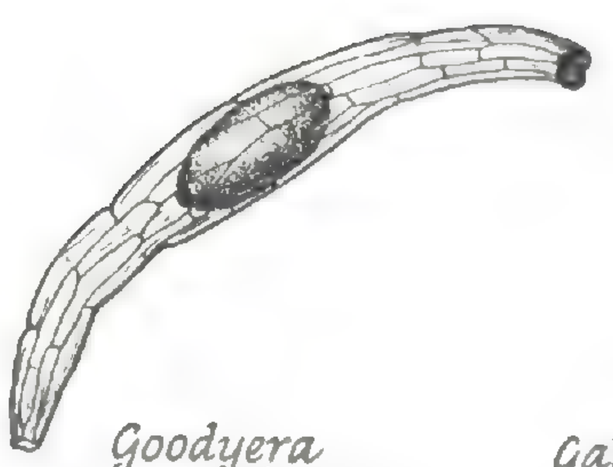
[1] It is noteworthy that, in addition to *Vanilla*, both *Selenipedium* and *Apostasia* possess aromatic substances. *Epistephium* and *Galeola* (Plate XI, A) of *Neottioideae* have also been reported to have essential oils in the fruits, but in lesser quantity. *Epistephium* and *Galeola* have the seeds provided with a prominent, transparent wing (probably a dispersal mechanism), but the embryo itself is enclosed by a sclerotic testa. *Vanilla*, *Epistephium* and *Galeola* p. pt. have been recognized as constituting a distinct family, *Vanillaceae*, on account of the characteristics mentioned above.

Plate XI

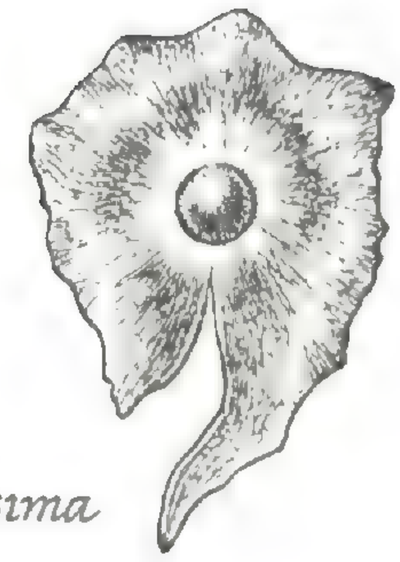
A



Calopogon pulchellus

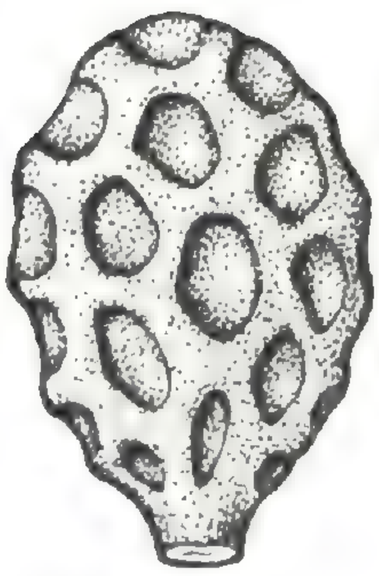


Goodyera pubescens

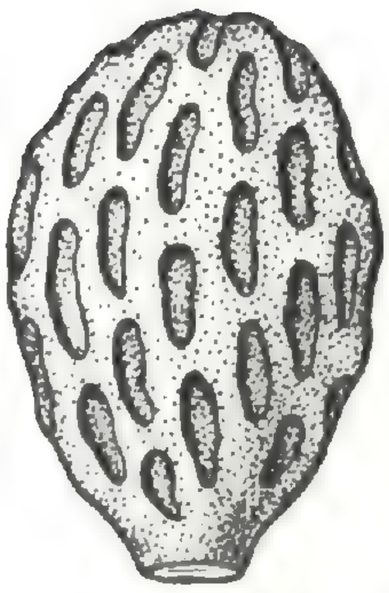


Galeola altissima

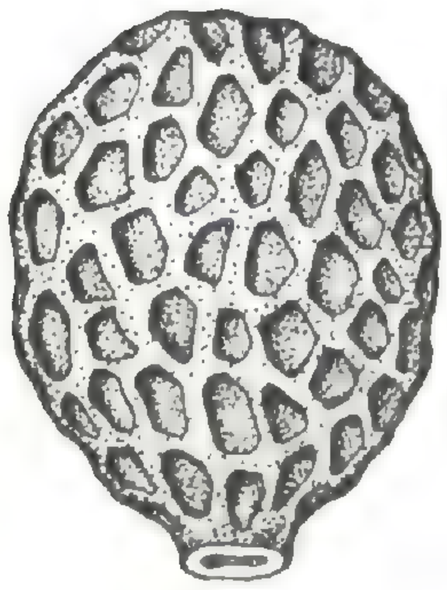
B



Apostasia nuda



Selenipedium Chica



Vanilla planifolia

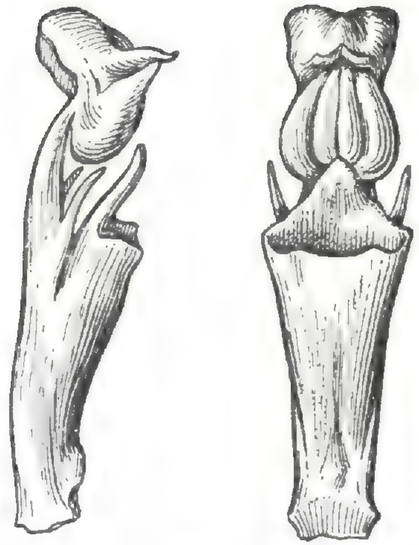
family, because in some of its members the fusion between stamens and style is only partial and the length of the adnation is relatively short. Indeed, in some species of *Neuwiedia* and *Apostasia*, the filaments of the anthers are partially recognizable, but this character is not even constant within a given genus. In *Apostasia papuana* (Plate XII), for instance, the filaments are completely obliterated or reduced to a mere connective tissue. In this respect *Cranichis crumenifera* (Plate XII) or any species of the genus *Spiranthes* or *Erythrodes* of the *Neottioideae* might likewise be removed from the Orchid family, because structurally the column is quite homologous in these taxa. Should we express the differences between families by a degree of adnation of these organs in millimeters?

The same incomplete fusion is also observable in *Vanilla anomala* (Plate XII) (*Neottioideae*) where the structure of the column is comparable to that of *Neuwiedia*, although only one anther is fertile, while the other two are expressed by the traces of the filaments as staminodes. *Vanilla anomala* exhibits a further important feature, viz., the versatile anther. This character, along with others, has also been marshalled to support the separation of the *Apostasioideae* into a distinct family. The occurrence of a versatile anther is not limited to this single species in the *Neottioideae;* there are a number of other genera and species which possess the same characteristic: e.g. *Cephalanthera*, *Psilochilus*, *Limodorum*, *Galeola*, *Didymoplexiella*, etc. In other instances, the anther is basifixed and attached rigidly to the column. *Vanilla Griffithii* var. *formosana* (Plate XII) clearly illustrates this situation, but a similar method of attachment is also present in several species of *Apostasioideae*.

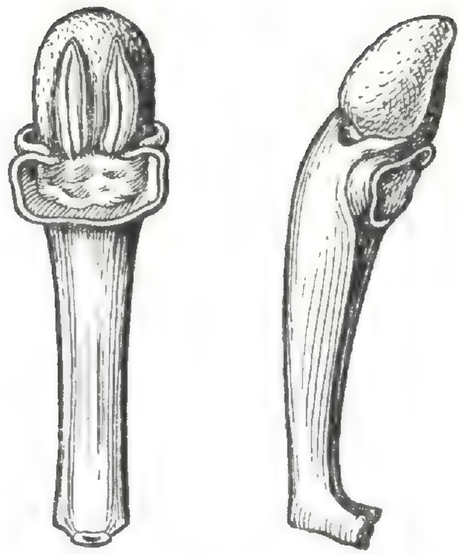
In viewing the other columnar structures as depicted on Plate XII, our attention is focused on another point of

Apostasia papuana

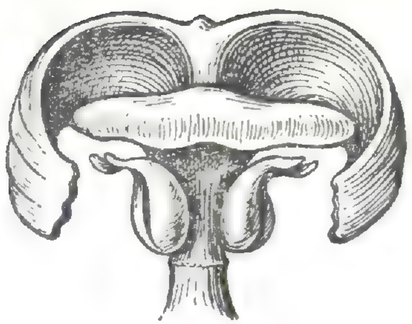
Cranichis crumenifera



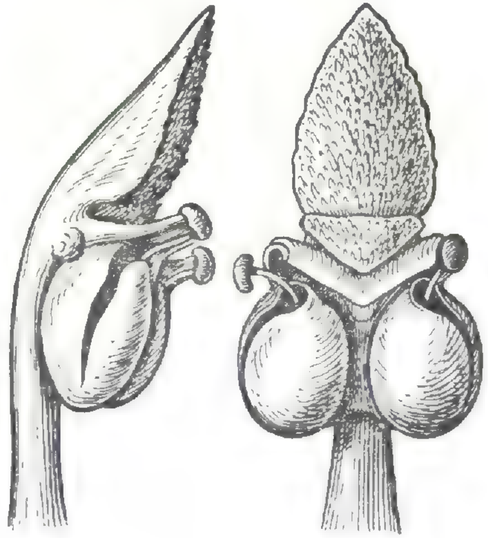
Vanilla anomala



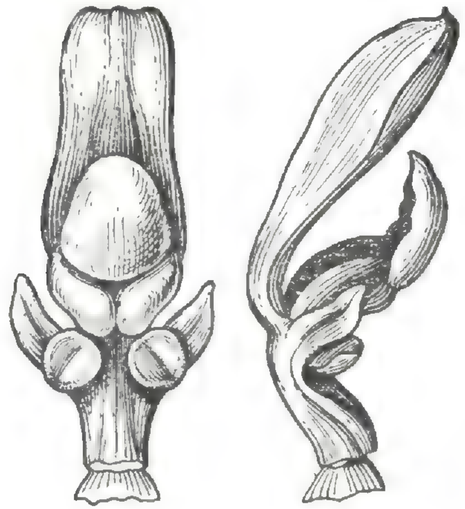
Cephalanthera alba



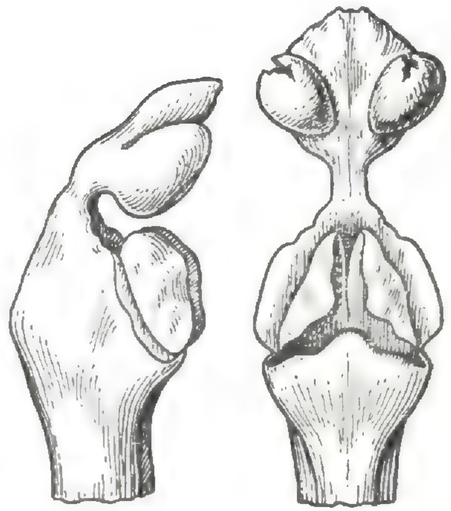
Corycium crispum



Satyrium saxicolum



Cypripedium Calceolus



Vanilla Griffithii var. formosana

significance, the position of the anthers in relation to the stigmas. Both *Apostasioideae* and *Cypripedioideae* have been distinguished from the monandrous orchids by the adnation of the anthers to the style at a level below the stigma. This criterion, however, may not be applied as an absolute rule, as it has been in the past, because, in addition to these groups, an extensive number of genera (ca. 50) in the *Neottioideae*, as well as the whole *Satyrium*-complex of the *Ophrydoideae*, exhibit a position of sub-stigmatic insertion of the anthers. Therefore, the criterion of the occurrence of such an insertion, which was also applied to justify the removal of *Apostasioideae* from the Orchid family, is invalidated.

The striking structural similarity of the column in both *Satyrium* and *Cypripedium* points to the convergent nature of the respective branches of the main lines of *Ophrydoideae* and *Cypripedioideae*. *Satyrium* itself represents a departure from the general monandrous orchid type in having two distinct anthers developed in the outer whorl of stamens (Pl. VIII, fig. 5). The fact that it is referred constantly to the monandrous orchids is, however, due to the nature of its pollinia.

Rostellum. One of the most significant features in the organogenesis of the column is the formation of a new or modified structure, the rostellum. The theoretical explanation of the origin of this organ, as postulated by Brown and Darwin, is widely discussed in various text-books; therefore, it is sufficient if we merely state that the median stigma during the reorganization of the flower has evolved into a new organ, the rostellum, with a specific function. It is the controlling and ensuring device for fertilization, since its position is located between the anther and the remaining stigmas; the pollinia are attached by a viscid secretion to the tip of this structure. Although this general situation is observable in the great

majority of orchids, transitional stages, as well as complete absence of it, are also well documented. In *Apostasioideae* and *Cypripedioideae* all three stigmas are fertile; therefore no rostellum is produced. In the remaining groups (*Neottioideae*, *Ophrydoideae* and *Kerosphaeroideae*) it is assumed that a rostellum must be present.

In some members of the *Neottioideae* (e.g. in the genera *Spiranthes*, *Goodyera*, *Erythrodes*, etc.) the style is modified into a wedge-shaped structure with the two separate stigmas situated laterally, while the third one is transformed into an elongate rostellum, all on the same plane. In this situation the nether surface of the rostellum is, however, still a functional stigma, as has been demonstrated by experimentation. We may look upon this condition as an intermediate step in the reduction or modification process, because in the more evolved members of the *Neottioideae* the rostellum ceases to be a functional stigma.

There are also a number of species in the *Ophrydoideae* without any reduction in number of stigmas. Several attempts have been made recently to explain the presence and origin in the *Ophrydoideae* of a so-called "rostellum" in addition to the three fertile stigmas. Since in the other groups (*Neottioideae* and *Kerospheroideae*) the gland of the pollinia is attached to the tip of the rostellum, it is believed that *Ophrydoideae* must also possess such a structure. Vermeulen postulated that the rostellum in the *Ophrydoideae* has an independent origin when all three stigmas are fertile, while Hagerup would derive the glands of the pollinia from the aborted lateral stamens of the outer whorl. I am unable to find a rostellum in the *Ophrydoideae* (comparable to that of the other groups); the structure which is generally called "rostellum" is merely a connective tissue between the two thecae of the anthers. Swamy in his studies of vascularization, has

shown that in *Habenaria* (*Ophrydoideae*) the compound stigma is supported by three vascular strands and in those species where the dorsal stigma is aborted, the supporting strand is obliterated simultaneously. Vermeulen's suggestion that the rostellum in *Bonatea* (*Ophrydoideae*) represents an elongation of the receptacle is hardly convincing, because of the appendicular nature of the column. To derive the viscid gland from the rostellum as a separate organ, or as a modified stigma, and the pollinia from the anther poses a situation rather difficult to comprehend. In my opinion, the whole structure of the pollinium originates as a unit from the anther; the gland itself is a transportation mechanism only. Furthermore, the nature of the anther and the pollinia in the *Ophrydoideae* is such that self fertilization is hardly possible. In those few species which are known to be autogamous, the presence of the connective tissue (whether or not representing a rostellum in reality) does not prevent self fertilization. Much research must yet be done with respect to developmental anatomy before a final conclusion as to the origin of the rostellum and the viscid gland may be drawn.

Indeed, at this point, it makes no difference which of the proposed theories is correct, because each of them bears out the same conclusion: the column of the *Ophrydoideae* is not derived from that of any of the other groups, but it is the product of an independent evolutionary line emerging from a polyphyletic complex.

Pollen. The pollen grains in orchids, at the time of shedding, are either single or more commonly united into tetrads, with or without aggregation into pollinia. In *Apostasioideae* and *Cypripedioideae*, as mentioned above, no pollinia are formed, but the sulcate or monocolpate microspores (similar to other Monocotyledons, e.g. *Hypoxis*) are always single at maturity.

In *Neottioideae*, the pollen grains cohere loosely into sectile pollinia (first step in specialization); in the advanced species, these are composed of microspores which are united into tetrads, while in the less evolved members (e.g. *Cephalanthera*, *Aphyllorchis*, *Lecanorchis*, *Galeola*, *Pogonia*, *Cleistes*, *Epistephium*, *Vanilla*, etc.), the pollinia are formed by single, either monocolpate, ulcerate or porate grains.

In the *Ophrydoideae*, with granular pollinia (second step in specialization) and *Kerosphaeroideae*, with hard, compact pollinia (final step in specialization), the pollinia are always composed of tetrads, which, depending on the position they occupy — whether along the periphery or towards the center—may be one of the five basic types: 1. tetrahedral; 2. isobilateral; 3. decussate; 4. T-shaped, or 5. linear.

The occurrence of single pollen grains and their aggregation into pollinia are in accord with the primitive or advanced status of the five main groups.

Discussion

I have attempted to demonstrate, in the diagram on Plate XIII, the correlation of the majority of criteria discussed in the foregoing paragraphs. The numbers beneath each name summarize, out of the 16 selected characteristics, the essential constitution of each group, and the numbers along the lines connecting these groups are those of characters shared.

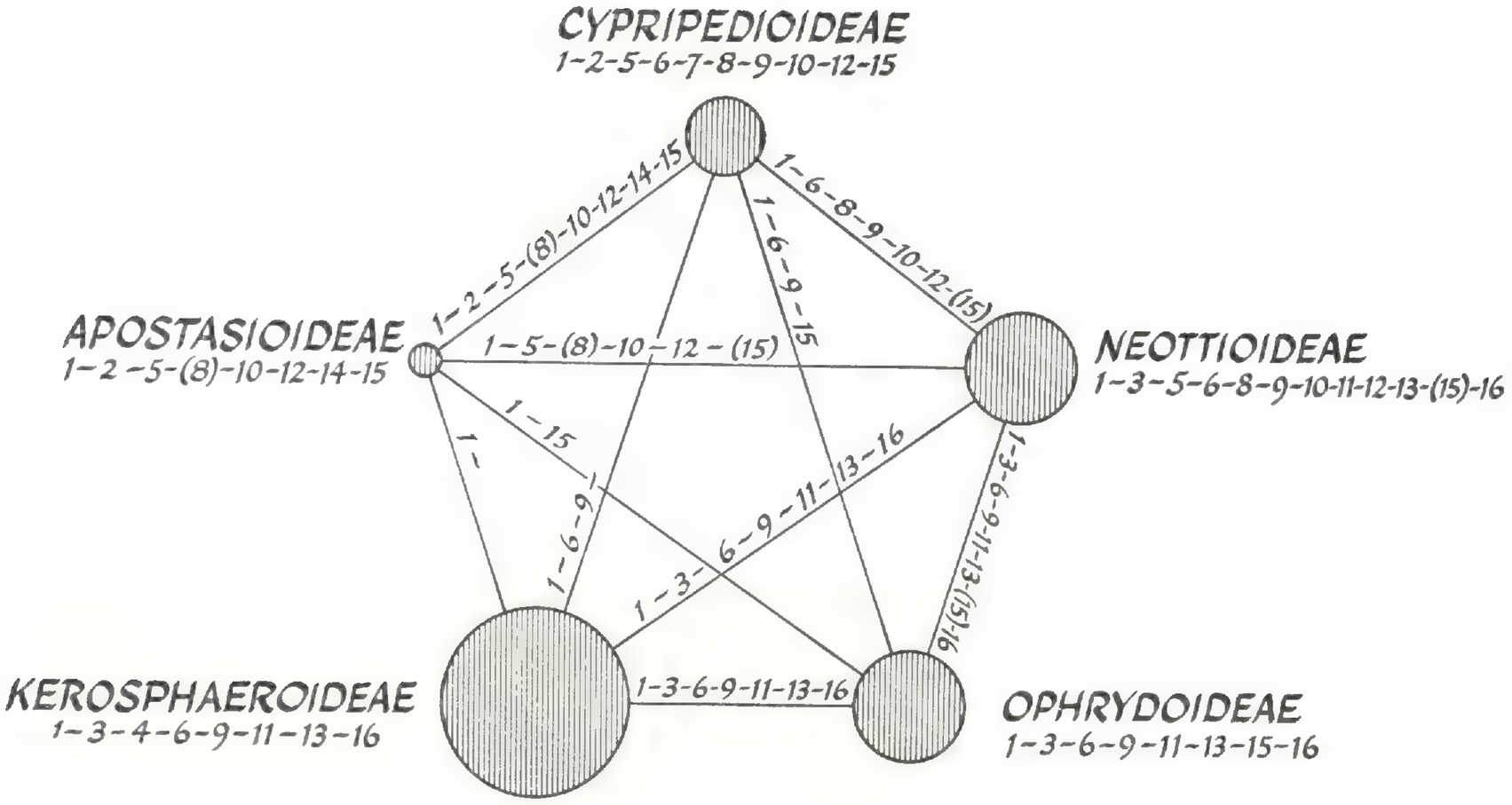
It has previously been stated that the dynamic and 3-dimensional structure of nature cannot be projected into a 2-dimensional perspective without destroying, or at best distorting, its salient features. This statement is relevant also to the diagram on Plate XIII. For the proper interpretation of this projection, we have to visualize each group (shaded circles) as a 3-dimensional unit

and the numbers, connecting each of these groups, as representing independent trends which originate from and link the groups at different points.

The sundry orchid systems proposed in the past were based essentially on progressive differentiation in a linear sequence, which assumes that the family is monophyletic in origin. Indeed, one's first impression is of a linear sequence from *Apostasioideae* to *Kerosphaeroideae*, especially when the groups are evaluated individually. When we attempt to assign a definite position and sequence to each of these groups, however, after studying their alliances, we find the linear arrangement to be rather absurd and unrealistic, since the groups are constantly in juxtaposition with each other. The pattern expressed by these interrelationships is reticulate and indicate that the family, as a unit, is polyphyletic in origin.

The general belief that, during the course of evolution, *Neuwiedia* (*Apostasioideae*) gave rise to both *Cypripedioideae* and the monandrous orchids, is hardly tenable. The so-called "clear cut" differentiation between *Diandrae* (*Apostasioideae* and *Cypripedioideae* together) and *Monandrae* is obliterated, as was mentioned earlier, by the presence of two anthers in the outer staminal circle of the *Satyrium*-complex in *Ophrydoideae*. In addition to this criterion, there are a number of characteristics common to both *Diandrae* and *Monandrae* which have been discussed above as well as documented on Plate XIII. I look upon each group as having an equal standing with respect to its adjacent group, and, for the purpose of classification, I am recognizing each as a distinct subfamily.[1] Perhaps some phylogeneticists may object to such a conclusion, but we have to bear in mind that each group is rather well circumscribed in spite of the close interrelationship.

[1] For the descriptions of these subfamilies see Appendix.



1. *Inferior ovary; ± fusion of ♂ and ♀ organs*
2. *6 vascular bundles entering floral axis*
3. *3 vascular bundles entering floral axis*
4. *2 vascular bundles entering floral axis*
5. *Axile placentation*
6. *Parietal placentation*
7. *Intermediate placentation*
8. *Embryo without a suspensor*
9. *Embryo with a suspensor (types I–V)*
10. *3 stigmas fertile*
11. *2 stigmas fertile, and rostellum formed*
12. *Pollen grain simple*
13. *Pollen grain compound*
14. *3 fertile anthers*
15. *2 fertile anthers*
16. *1 fertile anther*

As was stated earlier, *Apostasioideae* is considered by most recent phylogeneticists to represent a distinct family and has consequently been removed to distant alliances, such as *Haemodorales* and *Liliales* by Hutchinson and Takhtajan respectively. It is obvious that if *Apostasioideae* is removed from the Orchid family, this procedure automatically demands also the separation of *Cypripedioideae*, as was suggested by Mansfeld, because of the absence of pollinia formation, different fertile staminal circles, etc. If *Apostasioideae* and *Cypripedioideae* are removed from this interrelated complex, the remaining groups, *Neottioideae*, *Ophrydoideae* and *Kerosphaeroidcae*, would also require a new family status, because the equilibrium between these five groups is destroyed. On the other hand, the relationship between *Cypripedium* (*Cypripedioideae*) and *Cephalanthera* (*Neottioideae*) is so close that to regard them as members of distinct families would defy our whole evolutionary approach to systematics.

When we study the origin and phylogeny of the Orchid family devoid of paleobotanical documentation, our analysis is strictly limited to the uncovering of primitive features in living species. Since our approach is based *a priori* on such terms as genus and subfamily, these higher categories will aid our investigation only if they represent expanded dynamic units, although it is almost impossible to visualize the occurrence of such units in nature. The various evolutionary forces which have shaped and brought about the present-day orchids obviously did not act upon the family or even on a given genus, but rather on the species, because a species is the only tangible unit in nature with potentialities to mutate or evolve. Therefore, it would not be surprising if an absolute delimitation of a family becomes impossible.

The structure of an orchid flower is definitively a de-

rived one, and several attempts have been made by sundry workers to visualize its prototype as having three free segments in each of the five whorls. This arrangement by itself suggests but one course of evolution: progressive differentiation in a linear sequence. The evolutionary makeup of the Orchid family, on the contrary, is indicative of a rather complicated origin, because in certain species characters of a primitive and advanced nature occur simultaneously. A striking example is *Vanilla* (*Neottioideae*). The plant itself starts out as a terrestrial (primitive), but soon climbs up to the tree-tops where it leads an epiphytic mode of life (advanced); its ovary has a parietal placentation (advanced) yet the seeds possess a heavy sclerotic seed coat (primitive) and the embryo is sometimes known to develop an endosperm (primitive). *Vanilla* itself may be considered an advanced type with respect to other members of the *Neottioideae*.

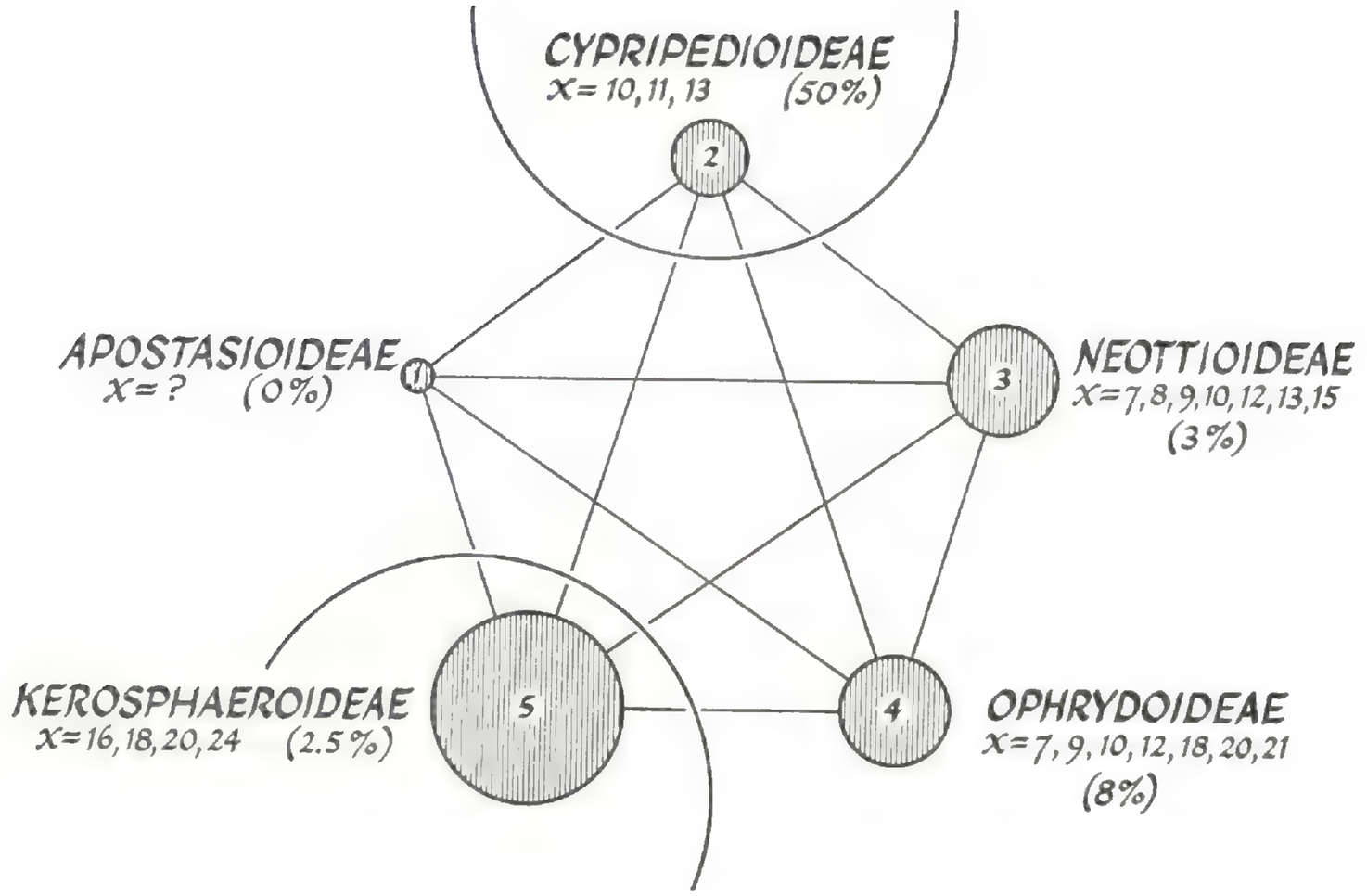
The association of primitive with advanced characters, which is to be found in each of the five groups, speaks rather clearly in favor of considering the Orchid family as one of those groups established relatively early during the evolution of the Angiosperms. Stebbins places its origin in the early Cretaceous Epoch and, on the basis of other evidence, I am inclined to agree with him. My studies of distribution, for example, based on deductive reasoning, lead to the same conclusion. The presence of the phenomenon termed pseudocopulation, noted in the *Ophrydoideae* and *Neottioideae*, may be mentioned here as further supporting evidence of age. If the Orchid family has evolved relatively recently, as some scientists postulate, such a precarious adjustment between the flowering time and the emergence of the fertilizing agents, as we find in the case of pseudocopulation, could hardly have come about. Nevertheless, I consider that the Orchid family is still in a state of evolutionary flux, and am in-

clined to believe that it has also undergone a rather sudden expansion during post Pleistocene time.

The manner through which the five main groups acquired their characteristics is impossible to determine without fossil evidence. The presence of primitive and advanced characters in the same species may, however, be an indication of fusion of independent evolutionary trends which very probably date back to a remote past, since cytological investigations and genetical experiments have demonstrated an absolute incompatibility of the groups. Whether or not this statement can be upheld without alteration in the future is hard to predict, inasmuch as the presently available information is very meager and unsatisfactory. Unfortunately, with respect to experimental genetics, only successful crosses are reported, while those which failed to "take" are carefully guarded from public possession and scientific scrutiny.

On Plate XIV, I have shown the results of a few crosses between *Cypripedioideae* and *Kerosphaeroideae*. Also I have on file certain data about attempted crosses between *Disa uniflora* (*Neottioideae*) and members of other groups, but since I am unable to ascertain the source of this data, I have omitted them in the diagram. The fact that the pollen is apparently unable to induce even parthenogenesis in the reported crosses between *Cypripedioideae* and *Kerosphaeroideae* may be a further indication of a remote origin of the respective groups.

The cytological coverage of the family is exceedingly poor. The known percentage of the chromosome counts of the species in each group is shown on Plate XIV. *Cypripedioideae* has a 50% coverage, due to the extensive studies in the genus *Paphiopedilum* by Duncan. The next highest is *Ophrydoideae*, a group almost exclusively of temperate regions, with 8% coverage based for the most part on European and Japanese species. Informa-



2 x 5 *Paphiopedilum x Cattleya — pollen dried, flower fresh*
2 x 5 *Paphiopedilum x Dendrobium — pollen rotted stigma away*
5 x 2 *Epidendrum x Paphiopedilum — column withered, pollen decayed*
2 x 5 *Paphiopedilum x Odontoglossum — a few chaffy ovules*

x = basic chromosome numbers
(%) = percent of species counted

tion about *Neottioideae* and *Kerosphaeroideae* is virtually lacking.

The known basic chromosome numbers for genera within each group are also included on Plate XIV. Hoffman, Duncan and Blumenschein have given the basic number of the Orchid family as x=20, calculated on the occurrence of this number in the majority of species of horticultural importance (*Ophrydoideae* and *Kerosphaeroideae*). Such a conclusion is, however, unwarranted, because the best we can hope for, with our present knowledge, is to suggest only the basic number for each of the groups.

The presence of an uninterrupted aneuploid series from n=10 to n=22 in the *Neottioideae*, and extensive polyploidy in the *Ophrydoideae* and to a lesser extent in *Kerosphaeroideae*, as well as the occurrence of euploid polyembryony in various groups, indicate a great genetic complexity in the family and, if this be fully exploited through further investigation and experimentation, it will contribute materially to our understanding of the origin and phylogeny of the *Orchidaceae* and probably go far towards full clarification of the many attendant problems.

Conclusion

The picture of the *Orchidaceae* which I have tried to present clearly demonstrates the great complexity of this family. The various degrees of specialization observable within each of the five groups make it rather difficult to trace the possible course of evolution. In the whole orchidaceous complex, *Neuwiedia* is, perhaps, the most primitive member, but even this taxon has to be considered as derived from more than one ancestor. In many respects, *Neuwiedia* is closely allied to the *Hypoxidaceae* and *Burmanniaceae*, with both of which it shares a pos-

sible origin, on the one hand with *Curculigo* and *Hypoxis*, and on the other with the leafy species of *Burmannia* (e.g. *B. longifolia*). *Apostasia* is hardly to be considered as a descendant of *Neuwiedia*, since its floral aspects and other morphological characters suggest rather a parallel course of development for both taxa. *Curculigo* and *Hypoxis* both have globular seeds with a sclerotic seed coat, as does *Apostasia; Neuwiedia* is characterized by an advanced type of seed with a loose testa. In addition to this characteristic, the non-saprophytic members of the *Burmanniaceae* show other primitive characters, such as axile placentation, monocolpate microspores, etc., which are also present in the *Apostasioideae*, *Cypripedioideae* and, to some degree, in the *Neottioideae*.

The presence of connecting trends between the *Orchidaceae* and its allies indicates that the family has been derived from other similarly complex groups and not, as often proposed, from any given family.

It is safe to assume that the Orchid family originated somewhere in the Asiatic tropics, possibly in Malaysia, because those species which possess primitive characteristics, and also the allied families, are native to that area.

The prototype of orchids, as Rolfe aptly wrote, may be visualized as "terrestrial monocotyledons, with an inferior ovary, numerous minute seeds having a reticulate seed coat and rudimentary embryo; the stamens and pistils are not yet aggregated into a column. The flowers were doubtless fertilized by insects, which on visiting the former, would become dusted with the pollen grains from the anthers as in the case of other entomophilous monocotyledons. We may also infer that the ancestral orchids were natives of great tropical region. The characters mentioned are found in the Malayan genus *Neuwiedia*, the most primitive of the existing orchids. The species of *Neuwiedia* have short, erect stems with a tuft of plicate,

Curculigo-like leaves and an erect spike of yellow flowers with nearly regular, connivent perianth, and three linear or oblong anthers borne on one side of the flower, free pollen grains and a slender nearly free style."

Appendix

The following descriptions of the five subfamilies mentioned in the text are herewith presented, according to the requirements set forth by the rules of the International Code of Botanical Nomenclature. The accompanying plates illustrate representatives of these groups.

Subfamilia **Apostasioideae** *Garay subfam. nov.*

(Plate XV). Flores zygomorphi; perianthii partes consimiles; filamenta antherarum stylo sive pro parte sive fere omnino connata, ergo columnam brevem formantia; antherae 2 vel 3, erectae, basi- vel dorsofixae interdum versatiles; pollen siccum granulosum; microsporae semper monocolpatae numquam in pollinium aggregatae; stigmata 3.

Typus: *Apostasia odorata* Bl.

Subfamilia **Cypripedioideae** *Garay subfam. nov.*

(Plate XVI). Flores zygomorphi; perianthii partes dissimiles; antherae stylo omnino adnatae, semper 2, tertia ex circulo exteriori staminodium formans; pollen viscosum, granulosum; microsporae semper monocolpatae, numquam, in pollinium aggregatae; stigmata 3.

Typus: *Cypripedium Calceolus* L.

Subfamilia **Neottioideae** *Garay subfam. nov.*

(Plate XVII). Flores zygomorphi; perianthii partes dissimiles (raro in *Thelymitra* fere consimiles); columna saepe abbreviata; anthera erecta, semper singula, basi- vel dorsofixa, interdum versatilis; microsporae sive mono-

colpatae vel ulceratae vel poratae sive tetradae in pollinia farinosa aggregatae; stigmata 2 vel 3, separata vel confluentia, tertium rostellum formans.

TYPUS: *Ophrys Nidus-avis* L.

Subfamilia **Ophrydoideae** *Garay subfam. nov.*

(Plate XVIII). Flores zygomorphi; perianthii partes dissimiles; columna saepa parva, cylindrica; antherae vulgo singulae, raro duae, thecis parallelis; microsporae tetradae semper in pollinia grosse granulosa aggregatae; stigmata 2 vel 3, semper confluentia, tertium saepe obliteratum, nunquam rostellum formans.

TYPUS: *Orchis morio* L.

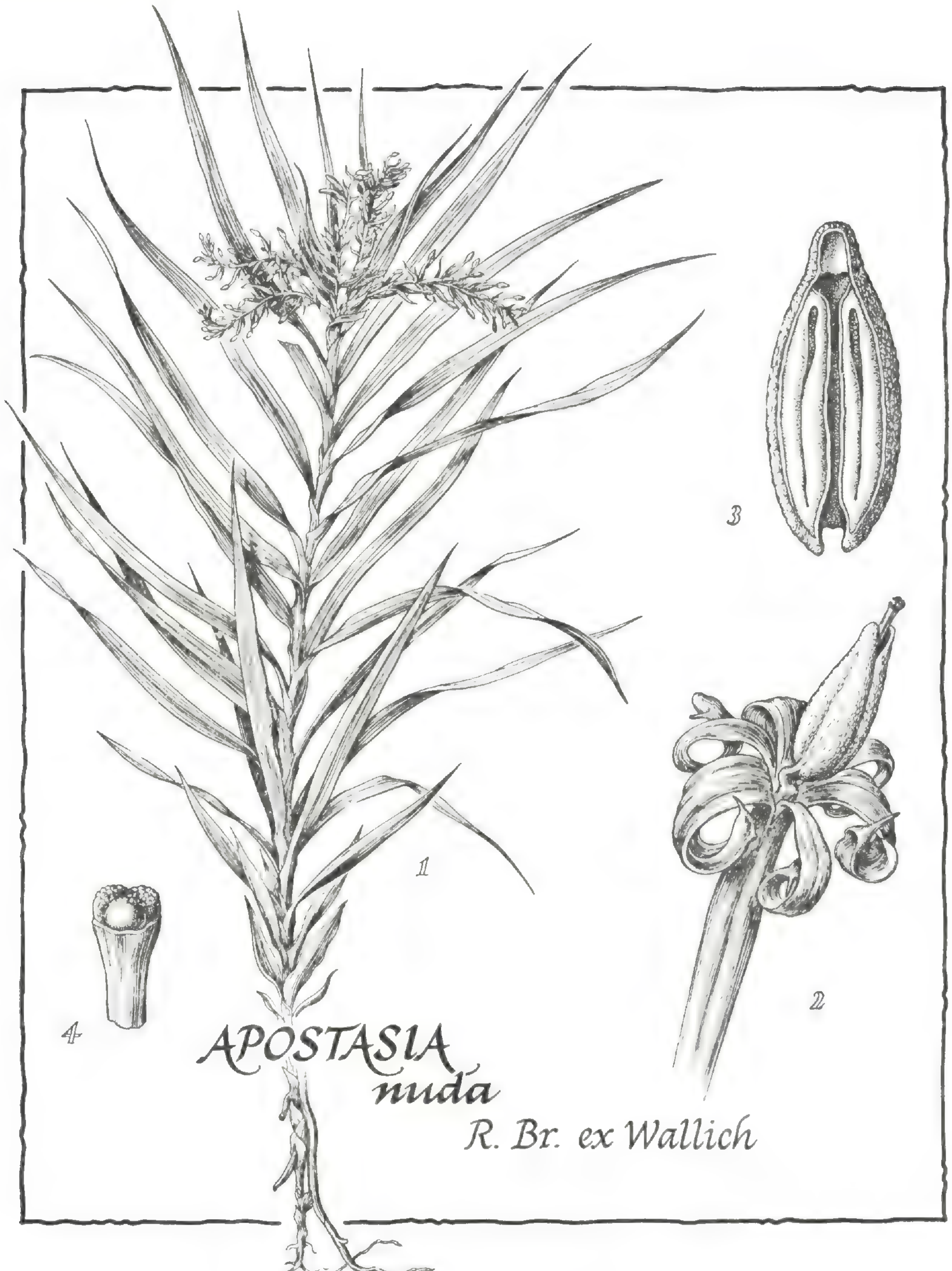
Subfamilia **Kerosphaeroideae** *Garay subfam. nov.*

(Plate XIX). Flores zygomorphi; perianthii partes dissimiles; columna valde evoluta; anthera incumbens vel dorsaliter reclinata, singula; microsporae tetradae in pollinia valde compacta aggregatae; stigmata 2, confluentia, tertium semper in rostellum modificatum.

TYPUS: *Epidendrum ciliare* L.

ACKNOWLEDGMENT

Part of the research upon which this paper is based was made possible through a grant from the National Science Foundation which is gratefully acknowledged.



APOSTASIA nuda

R. Br. ex Wallich

APOSTASIOIDEAE

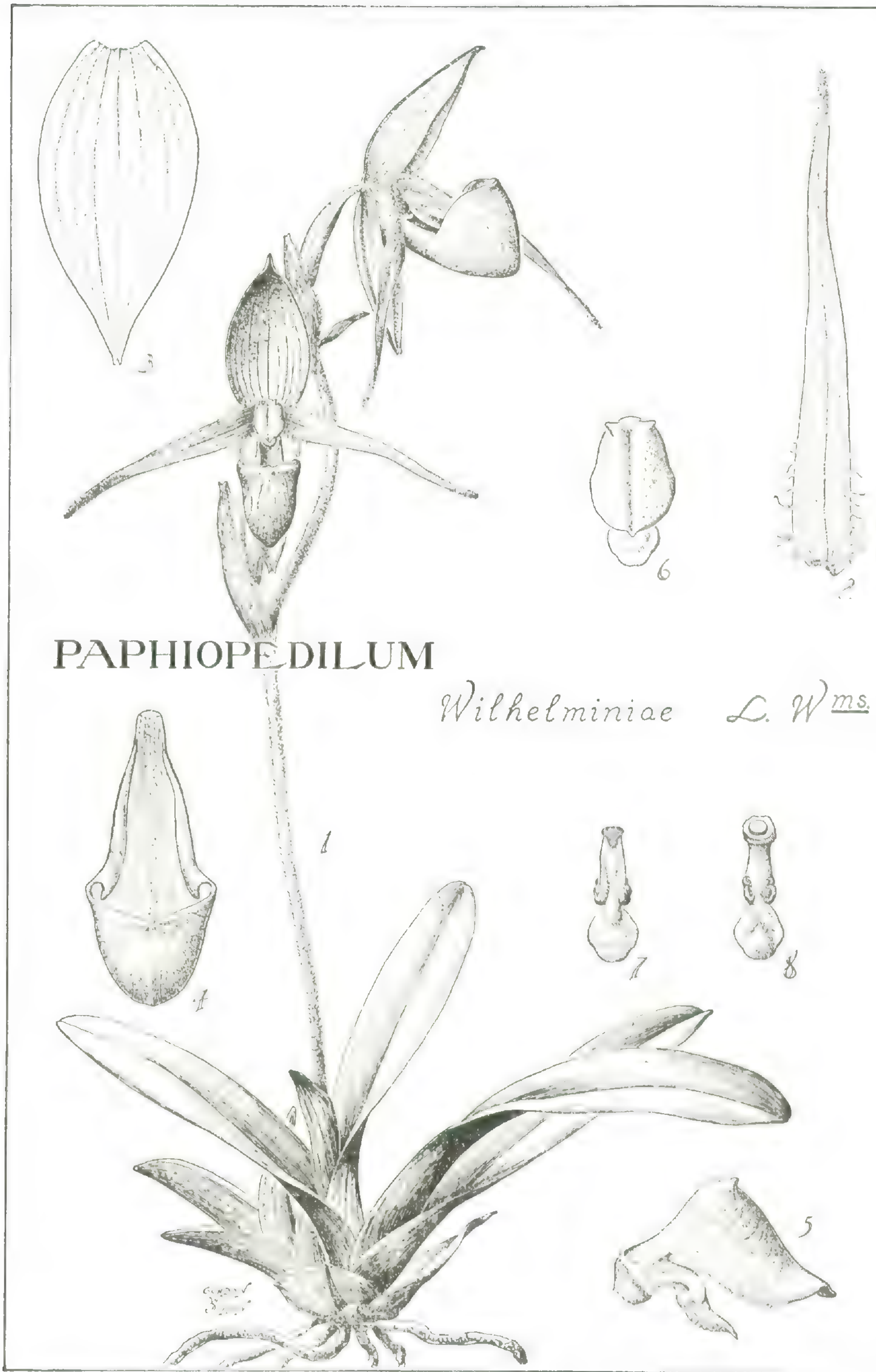
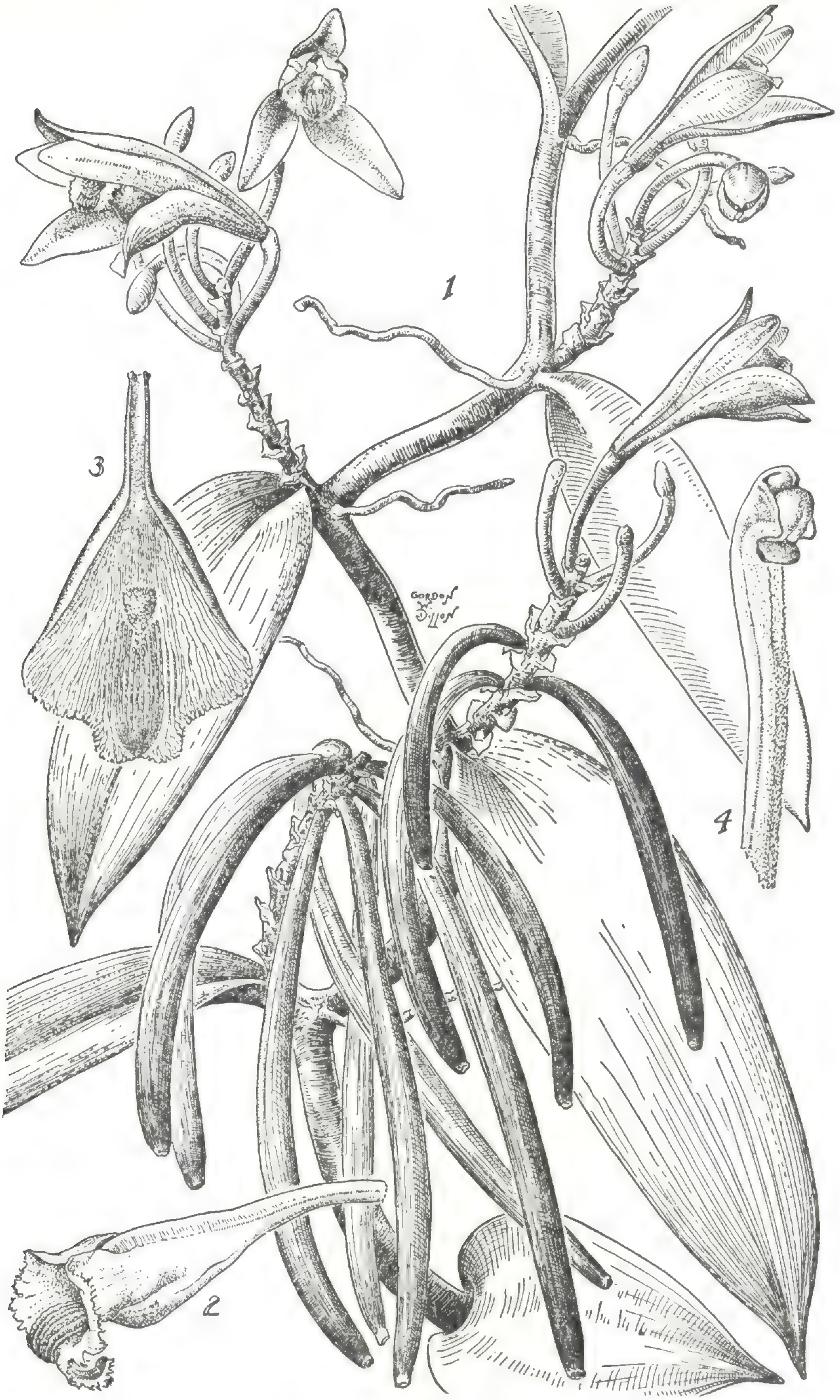

3
6
2
PAPHIOPEDILUM
Wilhelminiae L. W ms.
1
4
7
8
5

Plate XVII



Vanilla planifolia Andr.

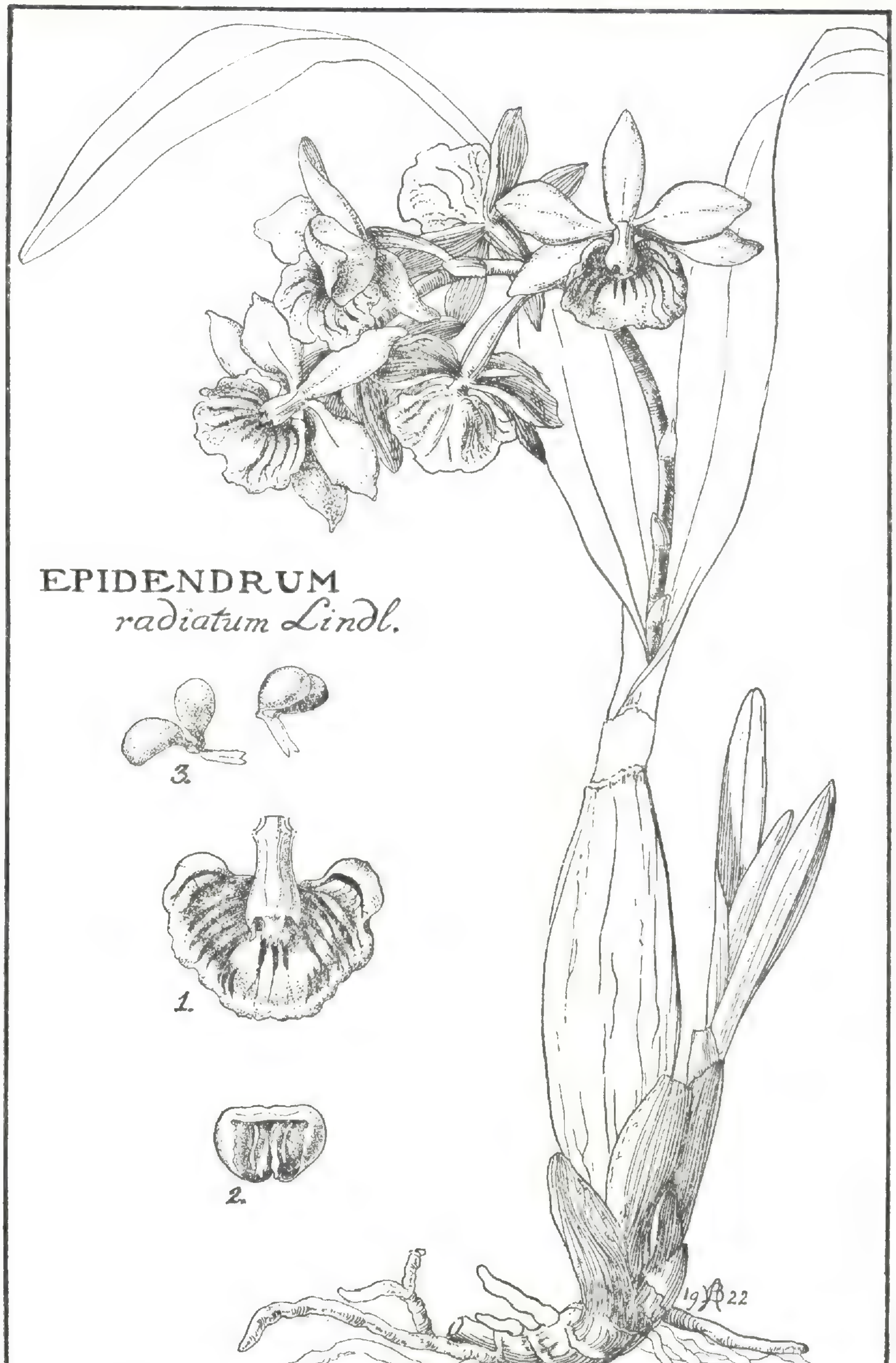
NEOTTIOIDEAE

Plate XVIII

Habenaria distans Griseb.

OPHRYDOIDEAE

Plate XIX



KEROSPHAEROIDEAE

SELECTED LITERATURE

1. Arber, A. 1925. Monocotyledons. Cambridge, The University Press.

2. Bauer, F. & Lindley, J. 1830–1838. Illustrations of Orchidaceous Plants. London, J. Ridgway & Sons.

3. Blumenschein, A. 1957. Estudos citólogicos na família Orchidaceae. Thesis (Mimeo.) Piracicaba, Brazil.

4. Burgeff, H. 1936. Samenkeimung der Orchideen. Jena, Gustav Fischer.

5. Darlington, C.D. 1945. Chromosome Atlas of Flowering Plants. George Allen & Unwin Ltd., London.

6. Duncan, R. E. 1959. Orchids and Cytology, in C. Withner: The Orchids, A Scientific Survey. New York, The Ronald Press Co.

7. Duncan, R. E. 1959. List of Chromosome Numbers in Orchids. ibid.

8. Eichler, A. W. 1875. Blütendiagramme. Leipzig.

9. Erdtman, G. 1952. Pollenmorphology and Plant Taxonomy. The Chronica Botanica Co., Waltham, Mass.

10. Hagerup, O. 1952. The Morphology and Biology of Some Primitive Orchid Flowers. Phytomorphology 2: 134–138.

11. Hirmer, M. 1920. Beiträge zur Organographie der Orchideenblüte. Flora, n.s. 13: 213–310.

12. Hoffmann, K. H. 1930. Beiträge zur Cytologie der Orchidaceen. Planta 10: 523–595.

13. Hurst, C. C. 1925. Experiments in Genetics. Cambridge University Press, London.

14. Hutchinson, J. 1959. The Families of Flowering Plants, ed. 2. Vol. II. Monocotyledons. Oxford University Press, London.

15. Lindley, J. 1836. A Natural System of Botany, ed. 2. London, Longman, Rees, Orme, Brown, Green and Longman.

16. Mansfeld, R. 1934. Orchideologische Mitteilungen II. Fedde Repertorium Sp. Nov. 36: 58–64.

17. Rolfe, R. A. 1890. A Morphological and Systematic Review of the Apostasiaceae. Journ. Linn. Soc. Bot. 25: 211–242.

18. Stebbins, G. L. Jr. 1950. Variation and Evolution in Plants. New York, Columbia University Press.

19. Swamy, B. G. L. 1948. Vascular Anatomy of Orchid Flowers. Bot. Mus. Leafl. Harvard Univ. 13: 61–95.

20. Swamy, B. G. L. 1949. Embryological Studies in the Orchidaceae II. Embryogeny. Amer. Midland Nat. 41: 202–232.

21. Takhtajan, A. L. 1954. Origins of Angiospermous Plants. Soviet Sciences Press. (Translation)

22. Vermeulen, P. 1955. The rostellum of the Ophrydeae. Amer. Orchid Soc. Bull. 24: 239–245.

23. Vermeulen, P. 1959. The Different Structure of the Rostellum in Ophrydeae and Neottieae. Acta Bot. Neerl. 8: 338–355.

24. Vogel, S. 1959. Organographie der Blüten Kapländischer Ophrydeen. Akad. Wissensch. u. Lit., Mainz; Abhandl. Mat. -Nat. Klasse; Nos. 6 u. 7.

ILLUSTRATION CREDITS

All plates and figures were drawn by Mr. Elmer W. Smith.

Plates VIII, XI, XIII, XIV, originals.

Plate IX, fig. 1, fig. 6, after Bauer & Lindley, Illustrations of Orchidaceous Plants.

fig. 2, fig. 3, after Pfitzer, Orchidaceae-Pleonandrae.

fig. 4, original.

fig. 5, after Müller and Kränzlin, Abbildungen der in Deutschland und den angrenzenden Gebieten vorkommenden Grundformen der Orchideen.

Plate X after Swamy, Embryological Studies in the Orchidaceae II.

Plate XII: *Apostasia papuana* after Smith, Nova Guinea XII, Orchidaceae.

Cranichis crumenifera and *Vanilla anomala*, originals.

Cephalanthera alba after Bauer and Lindley l.c.

Corycium crispum and *Satyrium saxicolum* after Vogel, Organographie d. Blüten Kapländischer Ophrydeen.

Vanilla Griffithii var. *formosana* after Ito, Icon. Jap. 1: t. 1, 1911.

Cypripedium Calceolus after Hegi, Ill. Fl. Mitteleuropas.

BOTANICAL MUSEUM LEAFLETS
HARVARD UNIVERSITY

CAMBRIDGE, MASSACHUSETTS, JUNE 30, 1960 VOL. 19, NO. 4

CYTOLOGICAL OBSERVATIONS ON TWO TROPICAL FORMS OF *TRIPSACUM*

BY

Y. C. TING[1]

SINCE the successful crosses between *Tripsacum dactyloides* L. and maize were reported by Mangelsdorf and Reeves in 1931, the genus *Tripsacum* has become more interesting to both taxonomists and geneticists. Despite this, only a limited number of species in this genus have been cytologically investigated (Longley, 1924 and 1937; Reeves and Mangelsdorf, 1935; Mangelsdorf and Reeves, 1939; Anderson, 1944; Graner and Addison, 1944; Dodds and Simmonds, 1946; Hernández and Randolph, 1950; Prywer, 1954; Maguire, 1957 and 1960). Most of the previous studies consisted of the determination of chromosome numbers and an interpretation of the homology between the chromosomes of *Tripsacum* and those of *Zea*. In addition, some discussed the phylogenetic relationship among different species in the genus (Mangelsdorf and Reeves, Anderson, and Graner and Addison).

The chromosome number of *Tripsacum laxum* Nash has been reported as about 2n=70 by Longley (1924) from a study of meiotic divisions. However, based on the mitotic divisions in the root tips, Mangelsdorf and Reeves (1939) stated that the chromosome number was 72.

[1] Research Fellow in the Bussey Institution, Harvard University.

Dodds and Simmonds (1946) described the meiosis in this species, and they also found that their material had 72 chromosomes in the root tips. They observed an average of 25 30 bivalents and 10 12 univalents and about two multivalents at diakinesis. They also observed noncongressed univalents and bivalents at metaphase I, laggards at anaphase I, and micronuclei at quartet stage. Finally, they suggested that *Tripsacum laxum* is an amphidiploid, and correlated the sterility of their plants with meiotic irregularity.

Cutler (1947) stated that *Tripsacum laxum*, as well as *T. pilosum* and *T. latifolium*, was usually sterile, and it did not produce any viable seeds.

As the result of a meiotic study on the Brazilian species *Tripsacum australe*, Graner and Addison (1944) concluded that it was a diploid. No knobs were observed on any of the chromosomes, although knobs frequently occur on the chromosomes in other species of the genus.

The present study consists of observations on certain meiotic features in two tropical Tripsacums from Colombia, probably referable to *Tripsacum laxum* Nash and *T. australe* Cutler and Anderson, respectively. It is hoped that it will provide some cytological bases for interpreting the phylogenetic relationships of the species concerned.

Materials and Methods

The clone of *Tripsacum laxum* was first collected near Buenaventura, Colombia, where it had been introduced from Puerto Rico. It is cultivated under the name *caña antigua*. The plants are unusually large and vigorous, even for *T. laxum*, with numerous stout tillers, but rarely set any viable seeds. The staminate spikelets are paired, with one sessile and one pedicellate spikelet. Presumably of hybrid origin, it seemed worthy of cytological investigation.

Tripsacum australe, the only native South American species of the genus, is found from Colombia to Bolivia, Paraguay and Brazil. It is very variable in habit. Little is known about its cytology. Graner and Anderson(1944) investigated a large robust clone from Mato Groso, Brazil, which had eighteen pairs of chromosomes and differed from all other species of *Tripsacum* in lacking terminal knobs on the chromosomes. Since further information regarding this species seemed desirable, a study was made of Colombian plants. These are smaller, with sessile paired staminate spikelets and they usually set fertile seeds.

Material of both these clones was collected for this study by W. H. Hatheway at the Estacion Experimental "Tulio Ospina" at Medellín during the summer of 1956. Inflorescences of the selected clones were fixed in the field in a freshly prepared mixture of three parts of 95% ethyl alcohol and one part of glacial acetic acid. Aceto-carmine squash technique was followed throughout the study.

Observations

Tripsacum laxum Nash

All of the stages of meiotic division, starting at pachytene, were found. Considerable difficulty was encountered in the identification of the chromosomes, because of the extremely irregular chromosome behavior at both pachytene and diakinesis. However, after a number of cells had been studied, it was concluded that this form of *Tripsacum* has 54 chromosomes and is a triploid. This conclusion was finally confirmed by chromosome counts of the tapetal cells in the anthers.

Not a single microsporocyte showed clearly all the chromosomes of the three chromosome sets. Through a number of separate measurements of different cells at

pachytene, the 18 chromosomes of a haploid set could be recognized. The length, arm ratio and spindle fiber attachment region of each chromosome were identified. There are probably three chromosomes (3, 5 and 8) having internal knobs on the long arm. The internal knob on the long arm of chromosome 3 is small and definitely heterozygous. The other two internal knobs are large and homozygous (Plate XX, figs. 1 and 2). Probably only chromosome 9 is knobless. The other 17 chromosomes have one or two knobs terminating one or both arms. However, there is a clear tendency to have the knobs terminating the long arms. Chromosomes 2, 3, 5, 14 and 17 are heterozygous for knobs and prominent chromomeres. In agreement with Longley's report (1937) on *Tripsacum floridanum*, chromosome 16 has a nucleolar organizer on its long arm. This condition is different from that in maize. Furthermore, the secondary constriction of the nucleolar chromosome in *T. laxum* is not always well marked.

Univalent chromosomes were frequently entangled with the bivalent chromosomes in a densely crowded mass. Whenever they were isolated, they demonstrated the spindle fiber attachment region and were readily identifiable. It was also observed that the univalent chromosomes sometimes formed a non-homologous association. Chromosome fragments and loops in the bivalent chromosomes were frequently found at pachytene. Fusions of the chromosome knobs and those of the spindle fiber attachment regions were constantly present.

At diakinesis, eighteen bivalent chromosomes were almost never found; the number of the univalent chromosomes was always greater than eighteen. Multivalent chromosomes were also seen, but only with a low frequency. At metaphase I, many chromosomes often failed to congress in the equatorial plate; the number of lag-

ging chromosomes found varied from eight to seventeen. Laggards at anaphase I were found in every sporocyte. As soon as the division process reached the quartet stage, several micronuclei were always produced around each quartet.

In every preparation, the microsporocytes in this form of *Tripsacum laxum* appeared much larger than those in the form of *T. australe* discussed below.

Tripsacum australe Cutler and Anderson

The pachytene chromosomes in the plants of this species were much easier to study. The number of bivalent chromosomes is definitely 18; in other words, it is a diploid with 36 somatic chromosomes. At late pachytene, spindle fiber attachment regions offered even better working material than those of maize chromosomes. Length and arm ratio of each chromosome could be averaged out as soon as several measurements had been made. Chromosome 8 has a small internal knob on the long arm (Plate XX, fig. 3). As illustrated in Plate XXI, chromosomes 1, 4, 11 and 15 have a knob terminating the long arm. The spindle fiber attachment regions of chromosomes 2, 10 and 16 appeared median. Knobs are not present on the short arms of any of the eighteen chromosomes.

As shown in Plate XXI, it is possible to divide the chromosomes into two groups, A and B; group A has the nine long chromosomes, and group B the nine short ones. The length of the shortest chromosome among the nine long chromosomes in group A is about equivalent to the length of maize chromosome 10. The length of the longest chromosome among the nine long chromosomes of the same group is about equivalent to the length of maize chromosome 4. Nevertheless, the arm ratios of most of the nine long chromosomes are differ-

ent from maize chromosomes of comparable length.

The pachytene chromosomes of this tropical form of *Tripsacum australe*, and those of the tropical form of *T. laxum*, as well, are, for unknown reasons, more heteropycnotic than those of maize, especially along the short arms of the nine short chromosomes.

Chromosome behavior was regular during all the stages of meiotic division. At diakinesis most of the homologues paired lengthwise, with occasionally one or two bivalents associated end-to-end. Univalents, however, were rarely found.

Discussion

One of the possibilities that may account for the origin of polyploidy in plants is by interspecific hybridization. The characteristics of the triploid form of *Tripsacum laxum* reported in this paper suggest that it probably originated in this manner. The evidence includes the following observations: (1) the pachytene chromosomes are heterozygous; (2) the chromosome behavior is extremely irregular at meiosis; (3) viable seeds are rarely produced; and (4) more univalents than trivalents are found at diakinesis.

In contrast to a triploid maize which Randolph and McClintock (1926) suggested had originated by the mating of two gametes with the chromosome number of one of them became doubled in premeiotic division, the present triploid form of *Tripsacum laxum* probably had a tetraploid *T. laxum* as one of its ancestors and an unknown diploid as the second parent. According to the observations of the pachytene chromosomes, these hypothetical parental species were, at least, different in chromosomes 2, 3, 5, 14 and 17. As stated in the foregoing section, these chromosomes were consistently found heterozygous for knobs and large chromomeres, and in addition, they often failed to associate regularly.

Plate XX

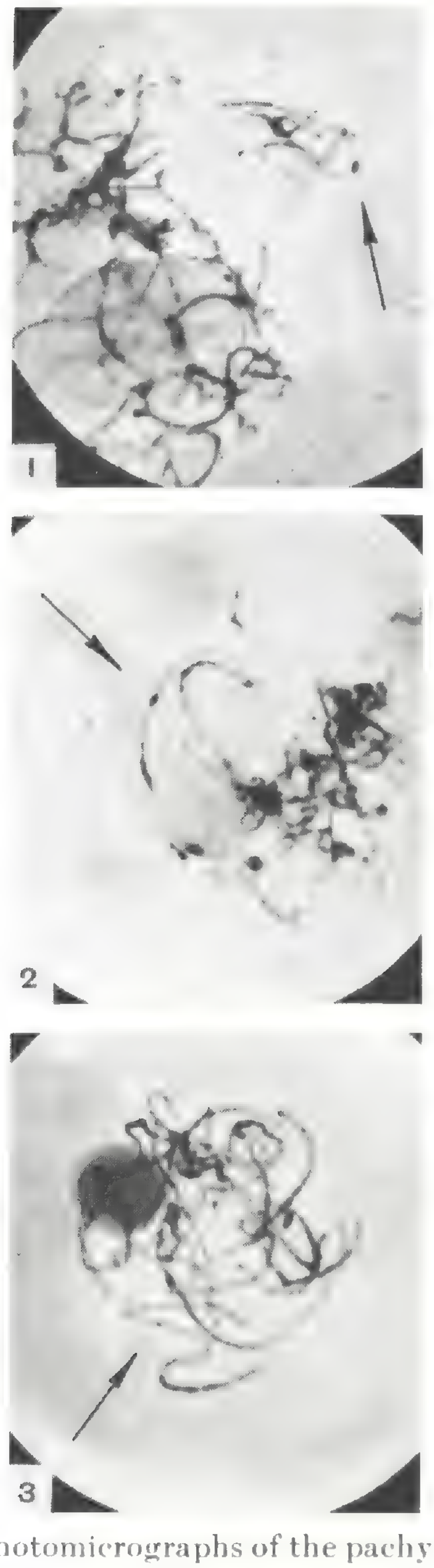


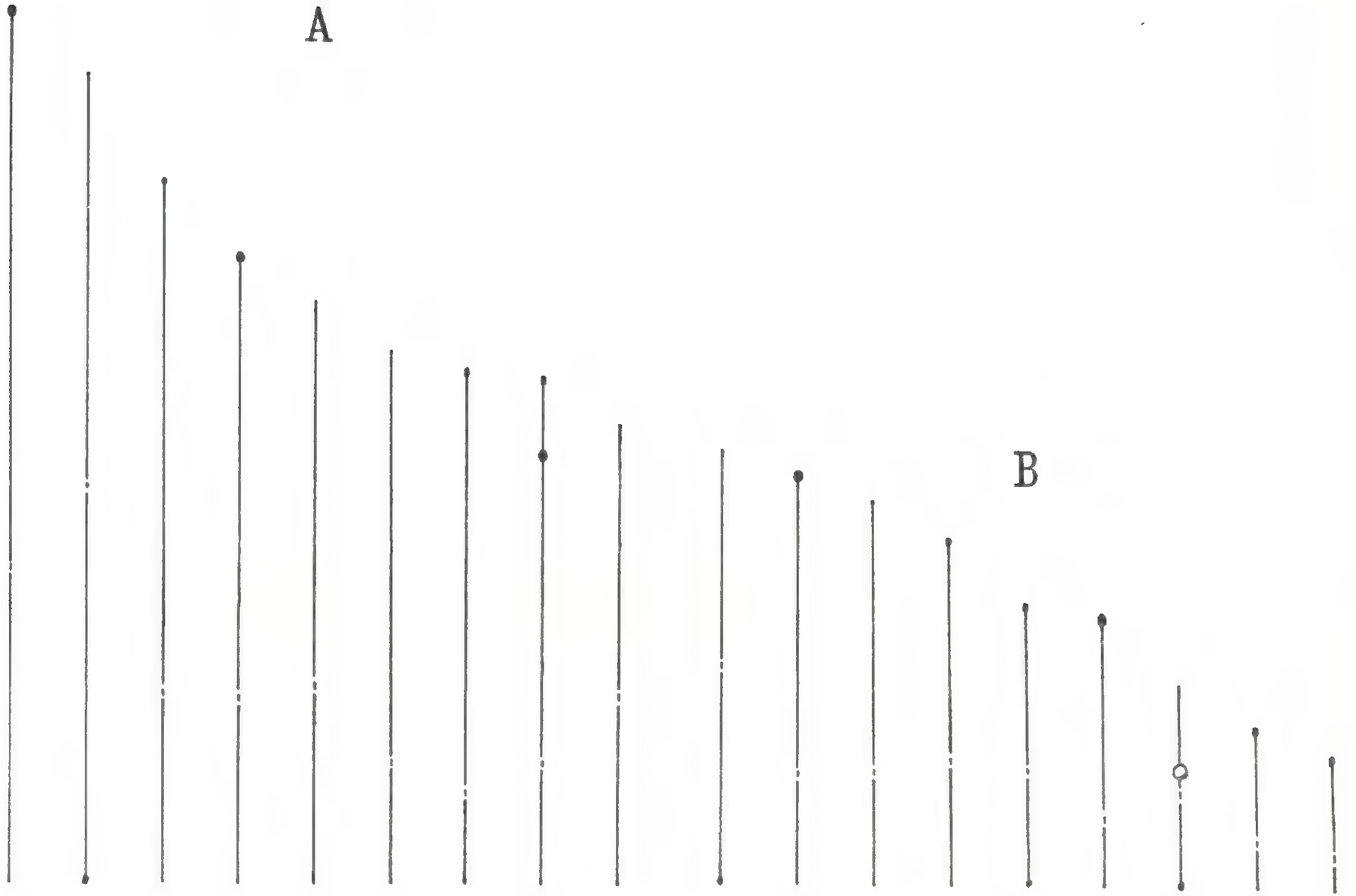
Plate XX. 1, 2. Photomicrographs of the pachytene chromosomes in the microsporocytes of triploid *Tripsacum laxum* Nash. The arrows indicate the internal knobs on the long arm of chromosome 5 (fig. 1) and on that of chromosome 8 (fig. 2). 750×.

3. Photomicrograph of the pachytene chromosomes in the microsporocyte of *Tripsacum australe* Cutler and Anderson. Arrow points to the internal knob on the long arm of chromosome 8. 750×.

EXPLANATION OF THE ILLUSTRATION

PLATE XXI. Diagram of the 18 chromosomes in *Tripsacum australe*. The lengths, arm ratios, spindle fiber attachment regions (broken line), large chromomeres (small dots), and knobs (large dots) of the chromosomes are determined by actual measurements and observations at pachytene in the microsporocytes. Chromosome 16 has a nucleolar organizer (circle) in the long arm. The chromosomes are divided into two groups, A and B: group A has the nine long chromosomes, group B, the nine short chromosomes.

PLATE XXI



Length (u)	68.8	66.0	57.1	52.5	45.3	42.8	42.0	40.4	37.5	34.1	32.6	31.0	26.6	23.1	22.0	16.0	13.2	10.8
Arm ratio (Long/Short)	1.7	1.0	2.8	2.8	2.0	3.4	4.8	3.4	1.4	1.0	2.9	2.5	1.8	1.5	3.3	1.2	2.7	3.8
Chromosome	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18

Sterility of the clone of *Tripsacum laxum* is undoubtedly due to irregular chromosome behavior at meiosis. Most of the resulting microspores receive more than the regular haploid number of chromosomes.

There is no evidence that *Tripsacum australe* was involved in the hybridization of the aforementioned triploid form of *Tripsacum laxum;* no marked chromosomes of the former were identified in the sporocytes of the latter. The form of diploid *T. australe* investigated is apparently different, however, in chromosome constituents from the one previously reported on by Graner and Addison (1944), since they did not find any knobs in their material.

Conclusions and Summary

The tropical form of *Tripsacum laxum* from Colombia is triploid with 54 chromosomes. The meiotic chromosome behavior was extremely irregular, and this phenomenon may serve as an explanation of the sterility of the plants. It is suggested that this tropical form of *Tripsacum* originated by interspecific hybridization between a tetraploid form of *T. laxum* and an unknown diploid.

A second tropical form of *Tripsacum* from Colombia, *T. australe*, is a diploid with 18 bivalents in the microsporocytes and 36 chromosomes in the somatic cells. Meiotic behavior of the chromosomes was regular. It apparently was not involved in the course of evolution of the triploid *Tripsacum laxum*.

Internal knobs which varied in size were observed in both of these tropical forms of *Tripsacum*. Also, in general, the short arms of the nine short chromosomes in both forms were more heteropycnotic than in those of maize. A diagram (Plate XXI) of the 18 chromosomes in *Tripsacum australe* is appended. The arm ratio and length of each chromosome are given.

Acknowledgments

The author wishes to thank Professor Paul C. Mangelsdorf for his advice and encouragement during the course of this study. He also expresses his appreciation to Dr. W. H. Hatheway, staff member of the Rockefeller Foundation Agricultural Program in Colombia, for providing the materials.

LITERATURE

Anderson, E. 1944. Cytological observations on *Tripsacum dactyloides*. Ann. Mo. Bot. Gard. 31: 317–323.

Cutler, H. C. 1947. A comparative study of *Tripsacum australe* and its relatives. Lloydia 10: 229–234.

Dodds, K. S. and N. W. Simmonds. 1946. A cytological basis of sterility in *Tripsacum laxum*. Ann. Bot. n.s. 9: 109–116.

Graner, E. A. and G. O. Addison. 1944. Meiose em *Tripsacum australe* Cutler e Anderson. (*T. dactyloides* subsp. *hispidum* Hitchcock.) Anais Escola supr. Agr. "Luis de Queiroz" 1: 213–224.

Hernández, Xolocotzi, E. y L. F. Randolph. 1950. Descripción de los *Tripsacum* diploides de México: *Tripsacum maizar* y *Tripsacum zopilotense* spp. Nov. Ofic. Estud. Esp. Soc. Agric. y Grand. Fol. Téch. No. 4: 1–28.

Longley, A. E. 1924. Chromosomes in maize and maize relatives. Jour. Agric. Res. 28: 673–682.

——. 1937. Morphological characters of teosinte chromosomes. Jour. Agric. Res. 54: 835–862.

Mangelsdorf, P. C. and R. G. Reeves. 1931. Hybridization of maize, *Tripsacum* and *Euchlaena*. Jour. Hered. 22: 329–343.

——. 1939. The origin of Indian corn and its relatives. Bull. Texas Agric. Exp. Sta. No. 574: 1–315.

Maguire, Marjorie P. 1957. Cytogenetic studies of *Zea* hyperploid for a chromosome derived from *Tripsacum*. Genetics 42: 473–486.

——. 1960. A study of homology between a terminal portion of *Zea* chromosome 2 and a segment derived from *Tripsacum*. Genetics 45: 195–209.

Prywer L., Czeslawa. 1954. Meiosis en *Tripsacum maizar* (H. & R.). Revist. Soc. Mex. Hist. Nat. 15: 59–64.

Randolph, L. F. and Barbara McClintock. 1926. Polyploidy in *Zea Mays* L. Amer. Nat. 60: 99–102.

Reeves, R. G. and P. C. Mangelsdorf. 1935. Chromosome numbers in relatives of *Zea Mays* L. Amer. Nat. 69: 633-635.

BOTANICAL MUSEUM LEAFLETS
HARVARD UNIVERSITY

CAMBRIDGE, MASSACHUSETTS, JUNE 30, 1960 VOL. 19, NO. 5

PRESTONIA: AN AMAZON NARCOTIC OR NOT?

BY

RICHARD EVANS SCHULTES AND ROBERT F. RAFFAUF

I.

THROUGHOUT the literature concerning native narcotic plants of South America may be found the statement that *Prestonia amazonica* (*Haemadyction amazonicum*), an apocynaceous vine, is the basic ingredient in the hallucinogen known as *yaje*. But many specialists, including most field investigators, have attributed *yaje* to sundry species of the malpighiaceous genus *Banisteriopsis*. They have been in essential agreement that *yaje* (of the westernmost Amazon of Colombia, Ecuador and a part of Peru, especially along the eastern slope of the Andes), *ayahuasca* (of Peru, Bolivia and part of Ecuador) and *caapi* (of the northwestern Amazon of Brazil and adjacent parts of Colombia) seem to be identical narcotics prepared from malpighiaceous plants.

That a member of the *Apocynaceae* might be employed in the Amazon as the source of a psychotomimetic drink is vitally important and would not appear to be an improbability. It was for this reason that Schultes (28), in 1957, reviewed the history of reports concerning *Prestonia amazonica*, keeping a sharp outlook for any well documented and botanically supported record. He concluded that while *Prestonia amazonica* is frequently

"named as the source of yaje and caapi. . . . there is little or no reliable evidence that this vine is ever employed, at least as the prime ingredient, in preparing the narcotic drink."

A chemical study, published shortly thereafter by Hochstein and Paradies (11), seemed, however, to end all uncertainty. Entitled "Alkaloids of Banisteria Caapi and Prestonia amazonicum" [sic], it reported that "the hallucinogenic plant *Banisteria Caapi* contains in addition to harmine, the alkaloids harmaline and *d*-tetrahydroharmine" and that "*Prestonia amazonicum* leaves have yielded another psychotomimetic amine, N,N-dimethyltryptamine." The plant materials studied by the two chemists were collected by Mr. D. H. Allen who was engaged in commercial activity in the vicinity of Iquitos, Peru. Both the *ayahuasca* (which is identified as *Banisteriopsis Caapi*) and the *yaje* (for which the determination *Prestonia amazonica* was offered) "were collected on the Napo River near Iquitos, Peru." Hochstein and Paradies state in a footnote that "the botanical identification was made by Dr. R. Ferreyra of the University of San Marcos, Lima." They do note parenthetically that these two vernacular names have, in the past, been cited as representing the same species, *Banisteriopsis Caapi*.

Nowhere in the paper, however, did the chemists state that voucher herbarium specimens, upon which a definitive identification could be based, had been sent in by the collector. Ferreyra (*in litt.*) informed us that he was not aware of the existence of any herbarium material in connection with these identifications. Faced with the lack of voucher specimens, the botanist often, in an attempt to be as helpful as possible in guiding the chemist, suggests a tentative identification based on a vernacular name, and the botanist's words of qualification are sometimes disregarded. This is precisely what has transpired in the pres-

ent case. We note that Hochstein and Paradies are careful to explain that the "second plant, 'yage'. . . . was made available to us as an aqueous extract of the leaves." This statement, together with the knowledge that the identification was not based upon herbarium material, leads us to believe that the aqueous extract was sent in directly from the field. It is probable, therefore, that the identification was made by tracing the vernacular name *yaje* which, in much of the literature, has, for some inexplicable reason, often been referred to *Prestonia amazonica.*

A significant observation from the chemist's point of view was made recently, when Raffauf and Folger (22) stated that the "reported occurrence of only one simple indole in the Apocynaceae to date is of sufficient interest to warrant some speculation. The structure looks enough out of place to suggest that the sample studied was not *Prestonia* at all, and indeed, N,N-dimethyltryptamine was isolated from an aqueous extract of leaves, the botanical origin of which appears to be in doubt. Confirmation of the presence of this alkaloid in an authentic specimen of the plant is certainly necessary." [1]

Because of the fundamental importance of a thorough and detailed understanding of the botanical sources of the New World narcotics, it seems advisable to us, in view of the existing confusion, to review the whole history of whether or not *Prestonia* is employed as an hallucinogen in the Amazon under the name *yaje.* In so doing, we realize that only further field work can be definitive. Such field work, nevertheless, should be attempted

[1] The possibility that an authentic specimen of *Prestonia amazonica* would yield N,N-dimethyltryptamine must not be excluded. Tryptamine is recognized as a possible intermediate in the biogenetic pathways to the harman-type alkaloids on the one hand (Malpighiaceae, Rutaceae) and many of the more complicated indole types (Apocynaceae) on the other. See R. Hegnauer, Planta Medica 6 (1958) 1).

with as clear a picture of the literature and other prior sources as possible.

II.

There is a complex of narcotics, usually attributed to malpighiaceous species of the genera *Banisteriopsis*, *Tetrapterys* and possibly *Mascagnia*, which has three widely employed vernacular names. *Caapi* is the Nhengatú or Tupí-Guaraní epithet used in the northwestern Amazon of Brazil and in the Comisaría del Vaupés in adjacent Colombia; according to Spruce (29), it is the word for "grass" and here means "thin leaf." *Ayahuasca*, signifying "vine of the dead," comes from Kechwa and is the accepted name of the hallucinogenic drink and its source plant in Peru, Bolivia and part of Ecuador. *Yajé*, a word of obscure linguistic origin and unknown meaning, is the name applied to the drink and the source plant along the eastern slopes of the Andes in Colombia and Ecuador and in those parts of Peru near the Colombian boundary.

In 1905, Rocha (25) published an account of his trip to the headwaters of the Ríos Caquetá and Putumayo in Colombia and reported that the natives employed as a narcotic a "little bush" or "leaves" called *yajé*. His account of its properties coincided very closely with those described for *ayahuasca*, and it was widely assumed that the two were identical as to the source plant.

In 1923, the Colombian chemist Fischer (6) reported that the *yajé* which he had analyzed and which had come from the Colombian Caquetá might, on the basis of anatomic and histologic species, be a species of *Aristolochia*.

Botanists who have worked in the Colombian Comisarías del Putumayo and Caquetá, where the drink is called *yaje*, agree that the prime ingredient is *Banisteriopsis*. The German collector, Klug (19), studied *yaje* there in 1929 and found only *Banisteriopsis* employed.

The same is true of the botanist Cuatrecasas (4), who studied the narcotic in the same area in 1939. The Colombian botanist García-Barriga (8), who has met with *yaje* in this and other areas, mentions only *Banisteriopsis* as the principal ingredient. Schultes has seen *yaje* prepared and has partaken of it on a number of occasions in the Putumayo and elsewhere in Colombia and has not seen used as the basic plant anything but a species of *Banisteriopsis*. The Russian botanists, Varanof and Juzepczuk, who studied the problem in the Colombian Caquetá in 1925–26, likewise found several species of *Banisteriopsis* employed either alone or together in preparing *yaje* (9, 10).

In 1956, the Brazilian chemist Costa (3) on the basis of isolation of the alkaloid yageine from species of the Amazon basin identified *yaje* with *Banisteriopsis Caapi*.

A suggestion that *ayahuasca* and *yaje* might be different plants seems first to have been advanced by the French anthropologist Reinberg (23). His study of tribes living between the Río Napo and Río Curaray in Peru led him to publish in 1921 the statement that the narcotic drink was an infusion of a few fragments of *ayahuasca*, a liana the diameter of a man's thumb, and leaves of *yaje*, "un petit arbuste, de lm. 50 de haut, á feuilles petiolées (petiole de 15 mm.), entières, ovales, longues de 20 cm., larges de 7 cm., regulières et terminées par une pointe de 2 cm." This description, of course, could very accurately be applied to a species of *Banisteriopsis*. Reinberg reported that his determinations were based upon specimens, but a search in the herbarium at Paris failed to disclose the existence of any herbarium material at the present time. He held that his specimens showed that *ayahuasca* and *caapi* were conspecific, representing *Banisteriopsis Caapi*, but that the *yaje* of the Río Curaray could, with reservations, be referred to *Prestonia*

(approaching, in some respects, *P. amazonica*) or a related apocynaceous genus.

In 1922, the Belgian horticulturist-explorer Claes (1,2) studied *yaje* amongst the Koregwahe Indians of the Comisaría del Caquetá in Colombia. He learned that the *yaje*, hitherto usually described as a "small bush" was an enormous forest liana, and he argued quite justifiably that those who had described it as a small bush had seen only young, cultivated individuals and not the vine in its wild state. Claes did not offer a botanical determination of *yaje*. He mentioned, however, that the Belgian botanist De Wildeman believed that it "might be" *Prestonia amazonica*. This would be most unusual, since, so far as we know, *Prestonia amazonica* does not become an enormous jungle liana. No voucher specimens were located in the Rijksplantentuin in Brussels, and Claes himself stated that he had not obtained material for identifying *yaje*. With this statement, we must assume that De Wildeman was voicing an opinion which he based on the information he was able to glean in the literature through the use of the vernacular name.

The pharmacologists Michiels and Clinquart (17) worked on the stems which Claes had collected. In 1926, they suggested—whether from their own observations or from the opinions of De Wildeman we do not know—that the stems appeared to belong to *Prestonia amazonica*. The same year saw the French pharmacologist Rouhier dismiss as "doubtful" the possibility that *yaje* could be referable to *Prestonia amazonica*.

In 1930, the French botanist Gagnepain (7) tried rather unsuccessfully to put some order into the chaos. He pointed out that 1) according to Reinberg, *ayahuasca* was "probably" *Banisteriopsis Caapi* but that *yaje* could not be referred to this species; 2) *yaje* seemed to approach *Prestonia amazonica*; 3) fragments received as *yaje* by

Rouhier in 1924 showed the plant to be an "opposite-leaved vine"; and 4) both Reinberg and Rivet sent in material which seemed to represent the same malpighiaceous plant.

Somewhat later, Gagnepain received through Rouhier a specimen from the Departamento de El Valle in Colombia, where the plant had been cultivated under the name of *yaje*. The provenience of the plant was unknown. The specimen had leaves and inflorescences. When Gagnepain discovered that it represented *Banisteriopsis Caapi*, he arrived at a most astounding conclusion: that *yaje* of Colombia was the same as *caapi* of Brazil but was not the same as *yaje* of Ecuador. He asserted that Ecuadorian *yaje* represented a different species of *Banisteriopsis* than did Colombian *yaje*. Thus, he appeared to drop *Prestonia amazonica* as the source of any *yaje*.

Most recently, Fabre (5), in reviewing the historical aspects of the identification of *ayahuasca*, *caapi* and *yaje*, concluded that all three are prepared basically from *Banisteriopsis*, even though other plants may be used as additives.

Several non-botanical workers, without the benefit of voucher specimens, accepted *Prestonia amazonica* as the source of the narcotic. Their "identifications" served to focus attention in the literature on the apocynaceous plant without really adding anything new of basic value. Reutter (24), for example, reported in 1927 that he had isolated yageine and yagenine from the vegetal parts of *yaje* or *ayahuasca*, which he referred to *Prestonia amazonica*. In a dictionary of Amazon plants, LeCointe (13) indicated his belief that the botanical sources of *ayahuasca* and *yaje* were two different plants, pointing out that some writers attributed *yaje* to *Prestonia amazonica*. In 1936, Pardal (19) stated that *caapi* was *Banisteriopsis*

Caapi and *yaje* was *Prestonia amazonica;* but the following year, he (21) attributed both to *Banisteriopsis Caapi.* The German toxicologist Lewin (14,15,16) named *Prestonia amazonica* as one of the plants possibly employed as an admixture with *Banisteriopsis Caapi.* In 1947, Sandeman (27) mentioned *yaje* casually and referred it to *Prestonia amazonica.* Most recently, the chemists Mors and Zaltzman (18), arguing that the alkaloid yageine is different from harmine, concluded, on the basis of a review of the literature, that *caapi* and *ayahuasca* are referable to *Banisteriopsis Caapi* but that *yaje* was not the same plant.

III.

All of the reports concerning the use of *Prestonia amazonica* as a narcotic stem directly or indirectly from the work of the British plant-explorer Richard Spruce. Spruce's meticulous field notes were written down in 1852 but did not see publication until, after his death, they were edited by Wallace and published in book form in 1908 (29).

Spruce was the first to identify the source of the *caapi* drink of the Rio Vaupés in northwestern Brazil as a species of *Banisteriopsis.* It was a new species and was originally described as *Banisteria Caapi.* The correct name is now *Banisteriopsis Caapi.* The description of this new malpighiaceous species was based upon a flowering specimen collected by Spruce himself. In his notes, however, Spruce stated that there was another kind of *caapi* in the same region and that it was called *caapi-pinima* or "painted caapi." In his original field notebook, preserved at the Royal Botanic Gardens at Kew, we find the following entry under "2712. *Banisteria Caapi* Mss. From this is prepared an intoxicating drink known to all the natives on the Vaupés by the name of *caapi.* The lower part of the stem, which is the thickness of the thumb

swollen at the joints, is the part used. This is beaten in a mortar with the addition of water and a *small* quantity of the slender roots of the Apocynac. (apparently a *Haemadictyon*) called *caapi-pinima* or painted *caapi*, from its lvs. being stained and veined with red. . . . Query? May not the peculiar effects of the *caapi* be owing rather to the roots of the *Haemadictyon* (though in such small quantity) than to the stems of the *Banisteria?* The Indians, however, consider the latter the prime agent, at the same time admitting that the former is an essential ingredient. The two plants are planted near all mallocas (villages). . . ."

When these notes were published in Spruce's "Notes of a botanist on the Amazon and Andes" (29), they suffered a slight change of emphasis. The terms of qualification disappeared. The published version states that *caapi-pinima* "is an apocynaceous twiner of the genus *Haemadictyon*, of which I saw only young shoots, without any flowers. The leaves are of a shining green, painted with the strong, blood-red veins. It is possibly the same species. . . . distributed by Mr. Bentham under the name *Haemadictyon amazonicum* n. sp. It may be the *caapi-pinima* which gives its nauseous taste to the *caapi*. . . . and it is probably poisonous. . . . , but it is not essential to the narcotic effect of the *Banisteria*, which (so far as I could make out) is used without any admixture by the Guahibos, Zaparos and other nations out of the Uaupés."

Spruce was one of the most meticulous of all scientist-explorers of South America. A less careful and botanically untrained observer might easily have confounded the young shoots of a *Prestonia* with *Banisteriopsis*, for the leaves of both are opposite, and the leaves of some species of *Prestonia* do resemble remarkably those of *Banisteriopsis* in shape and texture. But Spruce could never have confused an apocynaceous plant, full of a

white latex, with a *Banisteriopsis*. He might have erred as to genus, for the genera of the *Apocynaceae* are often hard to distinguish even with flowers. But even this possibility would seem, in the case of Spruce, to be rather remote. Schultes, on his long collection trip along the Colombian and Brazilian course of the Río Vaupés, searched for an apocynaceous vine growing around Indian huts, as described by Spruce; although every Indian *Manihot*-plot boasts its several cultivated plants of *Banisteriopsis*, nothing resembling a *Prestonia* was ever seen under cultivation.

A careful reading of Spruce's notes reveals the fact that he never claimed more for *Prestonia* or *caapi-pinima* than the role of a plant used as an admixture. We know from the reports of later workers that other plants are sometimes added in minute amounts to the drink prepared from *Banisteriopsis* in the belief that they change the attributes or properties of the narcotic drink. Schultes (28) reported the admixture of leaves of an apocynaceous tree, possibly *Malouetia Tamaquarina*, amongst the Makuna Indians of the Río Popeyacá of Colombia. Later writers, without herbarium specimens to back their claims, and taking their cue from Spruce whose notes they misread or misunderstood, have proposed that the narcotic drink in one part of the Amazon where it is known as *yaje* is prepared exclusively from *Prestonia amazonica*. For this assertion there is absolutely no basis in field work.

Prestonia amazonica is known from only one collection, the type collection made by Spruce in 1859 at Trombetas on the lower Amazon. In more than a century, the species has never been found again. We are forced, consequently, to believe that *Prestonia amazonica* is either a very rare species or else a strict endemic, confined to the general area where the type was collected. The Rio

Trombetas lies more than 1200 miles in a straight line from the eastern slopes of the Colombian Andes, where we are expected to believe that the natives are using this rare species in relative abundance as the source of their frequently employed *yajc*. The chances that *Prestonia amazonica* is used are, for all practical purposes, non-existent; and there seem to be no indications that any species of *Prestonia* is so employed along the eastern slopes of the Colombian and Ecuadorian Andes. Even in the area where Spruce reported its possible use a hundred years ago, there is all probability that it was employed solely as an admixture with *Banisteriopsis Caapi*.

In the region through which the Río Vaupés flows, the Indians distinguish two kinds of *caapi*. Spruce reported the minor *caapi* to be called locally *caapi-pinima*. Koch-Grünberg (12) found that the Tukanos of the Vaupés know two kinds, but he could identify only one. In 1948, Schultes (28) discovered the Indians on the Rio Tikié, a Brazilian affluent of the Uaupés, preparing a narcotic drink from the malpighiaceous genus *Tetrapterys*. He described the new species *Tetrapterys methystica* on the basis of a flowering specimen from the forest liana. From the bark a definitely hallucinogenic drink was prepared. The drink was rather yellowish, unlike the usually chocolate-brown of the drink prepared from *Banisteriopsis Caapi*. One wonders whether or not the term "painted caapi" could be applied to the kind of *caapi* that makes the unusual yellow drink. Be that as it may, the drink prepared from *Tetrapterys* represents probably the second kind of *caapi* reported by Koch-Grünberg in 1909.

Summary

While we are careful to point out that further field work, especially in Spruce's area along the Brazilian Rio

Uaupés, should be encouraged partly in an attempt to locate the use in *caapi* of a species of *Prestonia*, we believe that enough is known at the present time to make, in summary, the following statements:

1) There is no botanical support, nor any reliable support in the literature, for the assumption that any species of *Prestonia* (least of all *Prestonia amazonica*) is employed as the prime ingredient in the preparation of *ayahuasca*, *caapi* or *yaje*.

2) There is no reliable reference except Spruce's that any species of *Prestonia* is employed even as one of the minor ingredients or admixtures with *Banisteriopsis*.

3) There is serious doubt that the indole N,N-dimethyltryptamine occurs in *Prestonia* and every probability that the recent report of its presence in this genus was due to an erroneous identification of the material under analysis.

REFERENCES

1. Claes, Florent. "Quelques renseignements sur les coutumes des corregujaes de Colombie." Bull. Soc. Americ. Belg. (Dec. 1931) 39.

2. Claes, Florent. "Chez les hiutotos et correguajes." Bull. Soc. Roy. Belg. Geogr. 56 (1932) 25.

3. Costa, Oswaldo de A. Rev. brasil. farm. 37 (1956) 481.

4. Cuatrecasas, José. "Prima Flora Colombiana. 2. Malpighiaceae." Webbia 23 (1958) 343.

5. Fabre, René. "Quelques plantes médicinales de l'Amerique Latine: leur utilisation thérepeutique." Rev. Gen. Sci. Pures Appl. 62 (1955) 49.

6. Fischer, Cardenas, G. "Estudio sobre el principio activo del *yagé*." Unpubl. thesis, Univ. Nac., Bogota (1923).

7. Gagnepain, F. "Observations sur le yajé." Rev. Bot. Appl. Colon. 10 (1930) 293.

8. García-Barriga, Hernando. "El yaje, caapi o ayahuasca." Univ. Nac. Col., no. 23 (1958) 59.

9. Hammerman, A. F. Bull. Appl. Bot. Gen. Pl. Breed. (1929) 165.

10. Hammerman, A. F. "Le yagé en Amazonie." Rev. Bot. Appl. Agric. Colon. 10 (1930) 600.

11. Hochstein, F. A. and Anita M. Paradies. "Alkaloids of *Banisteria Caapi* and *Prestonia amazonicum*." Journ. Am. Chem. Soc. 79 (1957) 5735.

12. Koch-Grünberg, Theodor. "Zwei Jahre unter den Indianern." 1 (1909) 298.

13. LeCointe, Paul A. "A Amazonia brasileira III. Arvores e plantas uteis." (1934) 70; 471.

14. Lewin, Louis. "Sur une substance envirante, la banisterine, extraite de *Banisteria Caapi*." Comptes Rend. Acad. Sci. 186 (1928) 469.

15. Lewin, Louis. "Gifte und Vergiftungen." Ed. 4 (1929) 687.

16. Lewin, Louis. "Phantastica—narcotic and stimulating drugs." (1931) 140.

17. Michiels, M. and E. Clinquart. "Sur les réactions chimiques d' identification de la yageine." Bull. Acad. Roy. Méd. Belg., s. 5, 6 (1926) 19.

18. Mors, Walter B. and Perola Zaltzman. "Sôbre o alkalóide de *Banisteria Caapi* Spruce e do *Cabi paraensis* Ducke." Bol. Inst. Quim. Agric., no. 34 (1954) 17.

19. Morton, C. V. "Notes on *yagé*, a drug plant of southeastern Colombia." Journ. Wash. Acad. Sci. 21 (1931) 485.

20. Pardal, Ramón. "Las drogas estupefacientes e ilusógenas del indio americano." Rev. Geogr. Amer. 3 (1936) 1.

21. Pardal, Ramón. "Medecina aborigen americana." Humanior, Secc. C, 3 (1937) 273.

22. Raffauf, Robert F. and M. B. Folger. "Alkaloids of the Apocynaceae." Econ. Bot. 14 (1960) 37.

23. Reinberg, P. "Contribution à l'étude des boissons toxiques des indiene du Nord-ouest de l'Amazone, l'ayahuasca, le yajé, le huanto." Journ. Soc. Americ. Paris, n.s., 13 (1921) 25; 197.

24. Reutter, [K.]. "Du yagé ou aya huesca." Schweiz. Apotheker Zeet. 25 (1927) 289.

25. Rocha, Joaquín. "Memorandum de viaje (regiones amazónicas)." El Mercurio (Bogotá) (1905) 43.

26. Rouhier, A[lexander]. "Les plantes divinatoires." Rev. Métapsych. (1926) 325.

27. Sandeman, Christopher. "Thyme and bergamot." (1947) 24.

28. Schultes, Richard Evans. "The identity of the malpighiaceous narcotics of South America." Bot. Mus. Leafl. Harvard Univ. 18 (1957) 1.

29. Spruce, Richard. "Notes of a botanist on the Amazon and Andes" [ed. A. R. Wallace]. 2 (1908) 414.

A REPUTEDLY TOXIC *MALOUETIA* FROM THE AMAZON

BY

RICHARD EVANS SCHULTES

ALONG the inundable forests of the uppermost Amazon River, one of the common understory trees is the apocynaceous *Malouetia Tamaquarina*. This species I found to be especially frequent along the small Amazonian tributary, Río Loretoyacu, in the Colombian "Trapecio Amazónico," in the vicinity of Leticia. It first attracted my attention during a study of *Hevea* and other laticiferous trees of that region in 1944, since its copious latex was often added to *Hevea*-latex as an adulterant.

What interested me most in my study of *Malouetia Tamaquarina* was the reputation which the fruits have as a poison. This reputation is widespread in the Leticia-area, and the many reports which I heard during my three-year stay in Leticia agree strictly in details.

According to the natives, the ripened fruit of *Malouetia Tamaquarina* is consumed by the *pajuíl* (*Nothocrax urumutum* (Spix)), a wild bird frequently seen under domestication in this part of the Amazon. The flesh of the *pajuíl* is a great delicacy which may be eaten at any time of the year. During the months of March through June, however, when *Malouetia Tamaquarina* is in fruit, the bones of the bird must not be thrown to the dogs, lest they poison the animal. This poisoning is of a curious kind: it causes immediate and violent upsetting of the digestive tract and, within four or five hours, a glassy-eyed stare and interference with normal muscular coordination of the legs. It sometimes may be fatal.

A recent study of apocynaceous alkaloids (Raffauf, R. F. and M. B. Flagler in Econ. Bot. 14 (1960) 37) indicates that alkaloids have not been reported from *Malouetia*. I have not seen this poisoning reported in the literature, and I encountered it only in the Leticia-area. An

incidental report appeared in one of my previous papers (Schultes, R. E. in Bot. Mus. Leafl. Harvard Univ. 16 (1953) 90). There would be every reason to give some credence to the reports because the *Apocynaceae* or Dogbone Family is known to have highly toxic members.

Malouetia Tamaquarina is called *cuchara-caspi* ("spoon tree") in the Leticia-area, as the soft wood was formerly whittled into spoons. Some local rubber tappers refer to it as *chicle*. The tree may attain a height of fifty feet, averaging between thirty and forty. The usually straight, cylindrical trunk, with a diameter of twenty inches, is covered with a brownish or ashy-purple bark. The crown is light and irregular. The tree blossoms profusely, bearing white to yellowish, fragrant flowers. The free-flowing latex has a sweet flavor but causes a slight burning of the tongue. The wood is soft and white.

There are several closely related species of *Malouetia*, and these may be similarly poisonous. *Malouetia nitida* Spruce is reported to be used as an arrow poison. Hare, H. A., B. Caspari and H. H. Rusby "National Dispensatory," Ed. 2 (1908) 213). The leaves of what appears to be *Malouetia Tamaquarina* are sometimes added to the narcotic drink prepared from *Banisteriopsis Caapi* in the Colombian Vaupés (Schultes, R. E. in Bot. Mus. Leafl. Harvard Univ. 18 (1957) 39).

Malouetia Tamaquarina extends from the Guianas across the northwestern Amazon of Brazil, Colombia and Peru. A recent segregate has been described: *Malouetia peruviana* Woodson (in Ann. Mo. Bot. Gard. 22 (1935) 259), but the differences seem to be trivial. *Malouetia furfuracea* Spruce of Amazonian Peru is likewise known by the vernacular name *cuchara-caspi*.

An attempt to study *Malouetia Tamaquarina* or a related species chemically would seem to be worthy of consideration.

COLOMBIA: Comisaría del Amazonas, Trapecio Amazónica, Río Loretoyacu. Altitude about 100 m. September–November, 1944. *Richard Evans Schultes 6034; 6083; 6112.*

BOTANICAL MUSEUM LEAFLETS
HARVARD UNIVERSITY

CAMBRIDGE, MASSACHUSETTS, JANUARY 9, 1961 VOL. 19, NO. 6

HOW WERE THE GLASS FLOWERS MADE?

A LETTER BY MARY LEE WARE

A WORD OF EXPLANATION

The Ware Collection of Blaschka Glass Models of Plants — popularly called the "Glass Flowers" — is undoubtedly the most widely known and appreciated public attraction at Harvard University. An estimated third of a million people annually visit the Botanical Museum where they are housed.

The question which visitors most frequently ask is: "How were these beautiful flowers made?" Another query often heard is: "Has the secret been lost — did it die with the makers?"

The truth is that there was no secret process employed by Leopold Blaschka and his son, Rudolph, the creators of the "Glass Flowers." Every technique used was known to glass workers of the period. According to Mr. Louis C. Bierweiler, former Curator of Botanical Collections at the Museum and for more than fifty years custodian of the models, Rudolph Blaschka expressed to him his regret that many people thought that his handiwork utilized secret processes; he insisted that his work represented art in which there is no room for secrecy or egoism.

Although there is no complete information on all steps in the manufacture of the models, we do have the description of part of the work in a letter from the late Miss Mary

Lee Ware of Boston to Professor Oakes Ames, then Director of the Museum. This letter not only contains significant remarks about the technique involved in the glass work but gives an intimate picture of the artist, Rudolph Blaschka, and his wife in their home. It was written on her last visit to the Blaschkas in 1928. Miss Ware, and earlier her mother, Mrs. Elizabeth C. Ware, financially supported the botanical work of Leopold Blaschka from 1877 to 1895 and subsequently Rudolph until his retirement in 1936. In 1893, the Wares presented the collection to the President and Fellows of Harvard College as a memorial to Charles Eliot Ware, M.D., of Boston, a member of the Class of 1834.

Miss Ware's letter is herewith reproduced almost in its entirety and with only minor editorial alterations. The original is preserved in the Botanical Museum.

R.E.S.

Dresden, Oct. 3rd., '28

Dear Professor Ames,

It seems easiest in this very long letter to separate the description of the glass work itself from the more personal part; so I have done this, and I will tell you about making the models later. I have been out to Hosterwitz, half an hour by auto, alone four times and have passed the whole afternoons, long ones, looking first at the models. It took two afternoons to see them. Then I inspected the work room and its contents and was shown all the great improvements made by the Blaschkas in the house since his marriage, and finally accepted their hospitality of tea and delicious cakes, a far better arrangement than the old one of spending a whole day and having two solid meals!

Both Mr. and Mrs. Blaschka received me most cordially at the little garden gate, and we looked at each other to see what time had done; that first day, I was daunted to see what seemed a little old man, legs that were not strong, very rounded, stooping shoulders and an exceedingly white face. He must have dropped nearly two inches in height, his hands were somewhat out of shape from rheumatism and were very trembling. However, I came to the conclusion that this was due partly or largely to excitement at seeing me again and anxiety as to what I should say about the models.

When I was ready to leave and said "Aufwiedersehen," he drew himself up with quiet dignity and said, "Well, Miss Ware, are you satisfied?" I said, "Yes, Mr. Blaschka, I am more than satisfied, and I do not see how anyone could feel otherwise." He looked intensely relieved at once, and the next time I went out, his color had returned, and, when she saw him, Miss Niklason thought he looked well and strong, barring the stoop

which, I suppose, is inevitable with such sedentary work.

His eyes are simply marvelous, piercing; and yesterday, while painting a leaf, he worked most of the time without glasses, and he is seventy-one! He speaks freely of his age, of the work which can possibly still be accomplished and of the fact that he is the only one in the world who can do it; which I think is true. You would never find another man who combined the scientific knowledge of many years' study of plant and animal life; the study of glass, its component parts and its possibilities, not merely book knowledge but derived from experiment as well; together with the power of concentration, mental and moral; the artistic ideal as a loadstar which has enabled him to forego everything called pleasure, except his wife. She is sweet and devoted to his ideal, too, has softened and broadened him, and so humanized him that he is much better fitted to come in contact with the world than the Rudolph Blaschka who came to America in 1896.

He is just as modest and absolutely honorable as he ever was, but now he has a sense of his own worth, his own unusual force of intellect and character; and there is everything to justify that. I asked him one day whether he was still applied to for models to be kept in Germany, and he said, "Oh yes." Professor Neumann, to whom he went for something at your suggestion, asked why he would not give them some of his work. I asked what he replied. "Oh," he said, "I told him that I worked for Harvard University, that I was a man of absolute honor so would make no change and was satisfied."

I found that Sunday was his one day of rest and, suspected, from previous knowledge, that he was not taking enough time for air and exercise and was perhaps working late in the evening. I extracted the information that lately he had taken little or no time for fresh air and had

been working evenings, sometimes till midnight. I remonstrated vigorously and told him he must not do so, but he only said Professor Ames wanted the models and tho't him very slow — that it was *impossible* for him to do such work any faster, that no man could. It had evidently worried him much; and I had to work hard to reassure him that you would not feel so if you knew him and could see him work, that I would explain to you and that he absolutely *must* stop evening work and get the necessary air and relaxation to keep himself in good condition.

He only regrets that all the groups of fungi, etc., are not complete, but he has had to do them as he could and when he could get the specimens, depending more or less on seasons, weather, etc. He hopes to send off some twenty-five models, sprays or plants with their sections, etc., by the middle of the month — I think it will be nearer the end, but perhaps not. I believe this includes all the pears, except the blossoms, and strawberries; whether more I do not know. Apples, plums, apricots peaches, cherries, are for the most part finished and ready for the sprays, with the leaves ready to paint, and the exquisite fruit blossoms ready for the branches. He thinks the rest can be shipped in the spring, some thirty more. The fruits are not so beautiful to look at as the flowers are, but they are marvellous, and how one man can sit hour after hour, putting in the gossamer veinlets, or all the myriad little dots and irregular brown patches, passes my understanding: you would say that years could not do it, or a lifetime. If he hurried or worked quickly, he would be insane.

I sat and watched his movements as he worked. The table is covered not only with implements but with trays of leaves, formed but not colored, bottles in which he can stand the glass stems with leaves while drying or

cooling, specimens of fungus-covered fruits or dried leaves for use as guides (for the most part he studies them without glasses), bottles with powdered glass for use as needed, and saucers for the enamel paints he makes of powdered glass. In spite of the slightly unsteady hand, his movements are quiet, deft, soft in laying down or taking up where speed or a miscalculated movement might ruin the work of hours. It is breathless to watch.

The first afternoon, I saw the pears in every stage of disease, sometimes the fruit only, sometimes leaves and branches also. The moulds were wonderful, and I think you will be delighted with them all, but, of course, I know nothing of fungi. He had magnified 250 times a section of mould which comes on bread — remarkable. The strawberries were fascinating — plants, fruit and moulds; also the result of frosts on the developing fruit. The apples, also, were good; the peaches in their present stage of development seemed to me less so, but the final varnish was not yet on, and they all looked rather glassy. It all leaves you breathless that anyone can and will do such work.

Mr. Blaschka's head and bearing are very expressive, and I wished I could catch a photograph of his profile as he stood for a few moments, a plaque with a model on it held in both hands. His whole expression of absorbed, concentrated study was worth keeping, had it been possible. His own garden is small but full of fruit trees from which he gets some of his material for work; and the rest he gets from large fruit orchards near by. He also has books on fungi and mushrooms, and is looking forward eagerly to the work for Professor Weston. He says the lamellae will be very difficult but that he can make them. In view of his advancing years and the uncertainty of health, I would suggest that Professor Weston make a list of those subjects which he wants most, those which

RUDOLPH BLASCHKA
June 17, 1857—May 1, 1939
Photograph taken in 1938

are most important, although, on account of weather, season, and materials, it may be impossible for Mr. Blaschka to follow the sequence exactly; still, it would be a guide.

It troubles me very much that he and his wife cannot come over to see his life's work now that you have the models so beautifully arranged, and he looks so eager and pathetic when I describe the *mise en scene*. They are very simple, unaffected, dignified people, and I hope sometime that I may be able to manage it if I can only keep well when I come home. It seems cruel not to, but, of course, they could not travel in our country on what they have. I find that he did not lose all his investments in real estate or mortgages, etc., but *all* in government investments.

One change in the character of his work and, consequently, in the time necessary to accomplish results since I was last here is very noteworthy. At that time, he bought most of his glass and was just beginning to make some, and his finish was in paint. Now he *himself* makes a large part of the glass and *all* the enamels, which he powders to use as paint. This he considers to be practically indestructible, except by force—so that, if we could come back in a thousand years, we would find form and color as today. He has *dozens and dozens* of little bottles with colored powders and little boxes labeled with colored enamels which he makes himself, and powders for paint. The colored enamels are beautiful and fascinating. Some pieces he exposed on his roof or under the eaves for over a year, winter and summer, and they did not change in any way! . . .

My last visit to Hosterwitz on October 6 was most happy. Miss Niklason went with me and enjoyed it as much as I did. Supper was excellent, informal and pleasant, and I regaled them with all the Museum gossip that

I could think up. Mr. Blaschka did some leaf work again and Miss N. felt just as I do, that it is a great experience to watch that man at work. His whole head and hands are a study, and he worked until it was about dark without turning on his electric light. She also felt that the work was enough to wear anyone's nerves to madness, the confined position and closed room being a part of it.

I told him again that he must stop evening work with late hours and must get out for air and exercise for a time every day, that it was not fair to his wife or himself, that it made no difference how long it took to complete the models and that I should tell you that I said so. She is 45 only and perfectly devoted to him, but nobody can keep fresh without a little fun. She said they used to come in to Dresden sometimes when first married but it had been a long time since they were there. I tried to get them in to supper and the opera but unfortunately had to give it up on account of a cold. I know it has given him a fresh start and fresh courage to see me. I have been out there five times and I am sure that I accomplished what I came for. I wish I could have run in oftener, for so few realize what he is doing and their lives are necessarily secluded tho' evidently they are on friendly terms with their neighbors.

And now a word about the way in which he works. I watched while he painted a peach leaf affected by a fungus.

Each leaf is formed of clear white glass, pulled and worked by simple instruments in the flame, and each point on the margin has to be pulled out separately from the hot glass, to make the crenate edge to the degree characteristic of the species.

The leaf remains attached to the long stem of glass, 12 inches perhaps, from which it has sprung, until the coloring is completed and annealed. Then it is separated

and the fine wire, necessary for the permanent stem, is attached, coated with glass, and the leaf is ready to be attached to the branch; this last I could not see, as it took from about three till half after five to color just three leaves and put ribs and veins in one, and then anneal it.

A green leaf would be made of green glass; the method of coloring would be the same for both.

The colors are made of powdered glass mixed (moistened) with a few drops of turpentine or. . . . carefully added to the powder in little china saucers and stirred with a fine camel's hair brush, which, finely pointed in the moist paint, is used to administer the color to the leaf also.

The undulations of the leaf have already been made in the white glass so the buff or yellow paint is brushed on perfectly smooth, several times, and, before it has wholly dried, a strip of pointed whale bone marks the main vein down the centre, and the pointed quill of one of the brushes is used to mark each rib. Then a little of the powdered glass is dusted on by a camel's hair brush, shaken off and dusted on again in spots. If the leaf is partially healthy, faintly colored green glass is applied to the healthy parts. The camel's hair brushes, larger or finer, then are drawn down the vein and the ribs over and over again to give the necessary strength to the vein of size and color and to emphasize, as needed, the ribs. Many, many times the delicate tip of the brush would only touch tiny spots on the lines which needed a thought more of color.

Then, with the most delicate touch of the finest pointed brush, the cob-web veins were drawn into the texture of the leaf, between and at the end of each rib, like fine etching perhaps, but almost more delicate, like a breath rather than a touch and absolutely exhausting to nerves

and patience to continue, till the leaf was completed and ready to anneal.

Two wicks in two cups of parafine were started in front of him, and the flames driven at each other horizontally, his face, nose and mouth, protected by a piece of asbestos.

He took the glass stem in his left hand and inserted the leaf between the flames, where they just met. The tip first, moving it constantly after it had become red hot, till the whole leaf was finished. He keeps his right hand free to manipulate the apparatus or the handle, or guide the leaf if necessary, as he turns and twists it in the flame. Not infrequently, the annealing starts a flaw in the glass, and the leaf breaks so that a great many are necessary to complete a branch. He says that there is far more nervous strain, and it is far slower and more difficult to make a leaf than to make flowers. Annealing the powdered glass, instead of simply painting it, makes the process slower and more dangerous, but the final result is much more permanent; in fact, the color cannot change, and nothing but violence can destroy the model. He can scratch and scrape a leaf with his penknife and it leaves not a mark.

There is additional labor which I did not see. Annealing leaves the glass glittering and shining, and that appearance he destroys by the application of a certain varnish; and he applies this to the flowers also after stamens and pistils are set.

I think he said that he no longer paints at all except with the powdered colored glass which he can anneal. Another complication is that *only a certain kind* of glass can be used for the foundation glass, as the others spring and destroy the coat of anneal. All this is new since I was here nearly twenty years ago. He told me then that he had not at all come to the end of the possibilities of glass work, and these latest models show it to have been true.

The fruits are made over a fine but *very strong* wire, and he says in some of them there is as much as a ½ lb. of glass. That process I have not seen. Most of the fruits I think are done and quantities of leaves on their glass stems ready for painting are in drawers. Some of the fruits are blown, but very few, for he dislikes blowing glass, and the fruits are like eggshells, too perishable for transport. There are one or two sprays, however, with fruit of both kinds on them, and you would never know the difference in their looks.

The large pears and apples looked to me hopeless to transport, for no wire could stay on them, and no paper hold against their weight. But he is confident that by pinning the stalk firmly above the fruit stem it will never move. He has ordered a very heavy weight for the cardboard boxes.

This certainly has been a "long letter," and I shall be very anxious to know if you receive it safely, but please do not feel obliged to write when you are tired and busy —much as I always enjoy your letters.

Please remember me to Louis and, with most cordial greetings to you and Mrs. Ames,

Very sincerely yours,

MARY LEE WARE

BOTANICAL MUSEUM LEAFLETS
HARVARD UNIVERSITY

CAMBRIDGE, MASSACHUSETTS, FEBRUARY 17, 1961 VOL. 19, NO. 7

THE HALLUCINOGENIC FUNGI OF MEXICO:

AN INQUIRY INTO THE ORIGINS OF THE RELIGIOUS IDEA AMONG PRIMITIVE PEOPLES*

BY

R. GORDON WASSON ‡

WHEN I received in Mexico your President's invitation to speak here today, I knew that your Committee had made an unorthodox choice, for I am not a professional mycologist. As the appointed hour approached my trepidation kept mounting, for I saw myself an amateur about to be thrown to a pack of professionals. But your President's gracious introductory remarks, however unmerited, have put me at my ease and lead me to hope that we shall all enjoy together a mushroom foray of a rather unusual nature.

Those of you who do not know the story will be interested in learning how it came about that my wife, who was a pediatrician, and I, who am a banker, took up the study of mushrooms. She was a Great Russian and, like all of her fellow-countrymen, learned at her mother's knee a solid body of empirical knowledge about the common species and a love of them that are astonishing to us Americans. Like us, the Russians are fond of nature—

*The *Annual Lecture* of the Mycological Society of America, Stillwater, Oklahoma. August 30, 1960. Revised.

‡ Research Fellow, Botanical Museum of Harvard University.

the forests and birds and wild flowers. But their love of mushrooms is of a different order, a visceral urge, a passion that passeth understanding. The worthless kinds, the poisonous mushrooms—the Russians are fond, in a way, even of them. They call these 'worthless ones' *paganki*, the 'little pagans,' and my wife would make of them colorful center-pieces for the dining-room table, against a background of moss and stones and wood picked up in the woods. On the other hand, I, of Anglo-Saxon origin, had known nothing of mushrooms. By inheritance, I ignored them all: I rejected those repugnant fungal growths, expressions of parasitism and decay. Before my marriage, I had not once fixed my gaze on a mushroom; not once looked at a mushroom with a discriminating eye. Indeed, each of us, she and I, regarded the other as abnormal, or rather subnormal, in our contrasting responses to mushrooms.

A little thing, some of you will say, this difference in emotional attitude toward wild mushrooms. Yet my wife and I did not think so, and we devoted a part of our leisure hours for more than thirty years to dissecting it, defining it, and tracing it to its origin. Such discoveries as we have made, including the rediscovery of the religious rôle of the hallucinogenic mushrooms of Mexico, can be laid to our preoccupation with that cultural rift between my wife and me, between our respective peoples, between the mycophilia and mycophobia (words that we devised for the two attitudes) that divide the Indo-European peoples into two camps. If this hypothesis of ours be wrong, then it must have been a singular false hypothesis to have produced the results that it has. But I think it is not wrong. Thanks to the immense strides made in the study of the human psyche in this century, we are now all aware that deep-seated emotional attitudes acquired in early life are of profound importance. I suggest

that when such traits betoken the attitudes of whole tribes or peoples, and when those traits have remained unaltered throughout recorded history, and especially when they differ from one people to another neighboring people, then you are face to face with a phenomenon of profound cultural importance, whose primal cause is to be discovered only in the well-springs of cultural history.

Many have observed the difference in attitude toward mushrooms of the European peoples. Some mycologists in the English-speaking world have inveighed against this universal prejudice of our race, hoping thereby to weaken its grip. What a vain hope! One does not treat a constitutional disorder by applying a band-aid. We ourselves have had no desire to change the Anglo-Saxon's attitude toward mushrooms. We view this anthropological trait with amused detachment, confident that it will long remain unchanged for future students to examine at their leisure.

Our method of approach was to look everywhere for references to mushrooms. We gathered the words for 'mushroom' and the various species in every accessible language. We studied their etymologies. Sometimes we rejected the accepted derivations and worked out new ones, as in the case of 'mushroom' itself and also of 'chanterelle.' We were quick to discern the latent metaphors in such words, metaphors that had lain dead in some cases for thousands of years. We searched for the meaning of those figures of speech. We sought for mushrooms in the proverbs of Europe, in myths and mythology, in legends and fairy tales, in epics and ballads, in historical episodes, in the obscene and scabrous vocabularies that usually escape the lexicographer; in the writings of poets and novelists. We were alert to the positive or negative value that the mushroom vocabularies carried, their mycophilic and mycophobic content. Mushrooms are widely

linked with the fly, the toad, the cock, and the thunderbolt; and so we studied these to see what associations they conveyed to our remote forebears. Wherever we traveled we tried to enter into contact with untutored peasants and arrive at their knowledge of the fungi—the kinds of mushrooms that they distinguished, their names, the uses to which they put them, and their emotional attitude toward them. We made trips to the Basque country, to Lapland, to Friesland, to the Provence, to Japan. We scoured the picture galleries and museums of the world for mushrooms and we pored over books on archeology and anthropology.

I would not have you think that we ventured into all these learned paths without guidance. We drew heavily on our betters in the special fields that we were exploring. When we were delving into questions of vocabulary, when we worked out an original etymology for a mushroomic word, we were always within reach of a philologist who had made of that tongue his province. And so in all branches of knowledge. Sometimes it seems to me that our entire work has been composed by others, with us merely serving as rapporteur. Since we began to publish in 1956, persons in all walks of life have come to us in increasing numbers to contribute information, and ofttimes the contributions of even the lowliest informants are of highest value, filling a lacuna in our argument. We were amateurs unencumbered by academic inhibitions, and therefore we felt free to range far and wide, disregarding the frontiers that ordinarily segregate the learned disciplines. What we produced was a pioneering work. We know, we have always known better than the critics, the flaws in ours, but our main theme, which we adumbrated rather diffidently in *Mushrooms Russia and History* in 1957, seems to have stood up under criticism. If I live and retain my vitality, you may see published over the

coming years a series of volumes, to be called perhaps *Ethnomycological Papers*, and, at the end of the road, there may be a new edition of our original work, reshaped, simplified, with new evidence added and the argument strengthened.

It would give me pleasure to enumerate the names of those to whom we are indebted, but how tedious the roll call would be for you who are obliged to listen! There is one name, however, that in this audience I must cite. For more than ten years, we have been collaborating closely with Professor Roger Heim, Membre de l'Institut, and on all matters mycological he has been our guide and teacher. For these many years, he has been the director in Paris of the Laboratoire de Cryptogamie and, even longer, editor of the *Revue de Mycologie*. More recently, he has also borne the burden of directing the Muséum National d'Histoire Naturelle, that renowned center for advanced teaching and research in the biological studies, one of the glories of French culture. But these titles to academic distinction, though themselves of the highest order, do not tell you the story. Vast as is his learning and his experience in field and laboratory, sound as is his judgment in the vexed problems that you mycologists face every day, formidable as he is in polemic, it is as a rare human being that I commend him to you. Patient with the beginner, inspiring as a teacher, model of generosity toward others, prodigious worker in field and laboratory, and classical stylist in the French language, who could be more delightful whether in his published writings, or as correspondent, or as companion in the field? In the presence of Roger Heim, the time-worn conflict between science and the humanities fades away. One senses that the field of science for him is merely the New World that civilized man, the exponent of the humanities, is exploring and assimilating. What guardian

angel had me in his keeping when, after the Second World War, I ascended the steps of his laboratory in Paris to meet him for the first time, a stranger, an American, an ignoramus in the complex, the vast, the exacting discipline that you and he share together? At once he made me feel at home and it was not long before he was developing enthusiasm for our ethnomycological inquiries. Later he became our indispensable and beloved partner in our Middle American forays.

I do not recall which of us, my wife or I, first dared to put into words, back in the '40's, the surmise that our own remote ancestors, perhaps 4,000 years ago, worshipped a divine mushroom. It seemed to us that this might explain the phenomenon of mycophilia vs. mycophobia, for which we found an abundance of supporting evidence in philology and folklore. Nor am I sure whether our conjecture was before or after we had learned of the rôle of *Amanita muscaria* in the religion of several remote tribes of Siberia. Our bold surmise seems less bold now than it did then. I remember distinctly how it came about that we embarked on our Middle American explorations. In the fall of 1952 we learned that the 16th century writers, describing the Indian cultures of Mexico, had recorded that certain mushrooms played a divinatory rôle in the religion of the natives. Simultaneously we learned that certain pre-Columbian stone artifacts resembling mushrooms, most of them roughly a foot high, had been turning up, usually in the highlands of Guatemala, in increasing numbers. For want of a better name, the archeologists called them 'mushroom stones,' but not one archeologist had linked them with mushrooms or with the rites described by the 16th century writers in neighboring Mexico. They were an enigma, and 'mushroom stone' was merely a term of convenience. Some of these stone carvings carried an effigy on the stipe, either

a human face or an animal, and all of them were very like mushrooms. Like the child in the Emperor's New Clothes, we spoke up, declaring that the so-called 'mushroom stones' really represented mushrooms, and that they were the symbol of a religion, like the Cross in the Christian religion, or the Star of Judea, or the Crescent of the Moslems. If we are right—and little by little the accumulating evidence seems to be in our favor—then this Middle American cult of a divine mushroom, this cult of 'God's flesh' as the Indians in pre-Columbian times called it, can be traced back to about B.C. 1500, in what we call the Early Pre-classic period, the earliest period in which man was in sufficient command of his technique to be able to carve stone. Thus we find a mushroom in the center of the cult with perhaps the oldest continuous history in the world. These oldest mushroom stones are technically and stylistically among the finest that we have, evidence of a flourishing rite at the time they were made. Earlier still, it is tempting to imagine countless generations of wooden effigies, mushroomic symbols of the cult, that have long since turned to dust. Is not mycology, which someone has called the step-child of the sciences, acquiring a wholly new and unexpected dimension? Religion has always been at the core of man's highest faculties and cultural achievements, and therefore I ask you now to contemplate our lowly mushroom—what patents of ancient lineage and nobility are coming its way!

It remained for us to find out what kinds of mushrooms had been worshipped in Middle America, and why. Fortunately, we could build on the experience of a few predecessors in the field: Blas Pablo Reko, Robert J. Weitlaner, Jean Bassett Johnson, Richard Evans Schultes, and Eunice V. Pike. They all reported that the cult still existed in the Sierra Mazateca in Oaxaca.

And so we went there, in 1953. In books and articles we have described time and time again our later adventures, and some of you, surely, are familiar with them. So far as we know, we were the first outsiders to eat the mushrooms, the first to be invited to partake in the agapé of the sacred mushroom.* I propose here this evening a new approach, and will give you the distinctive traits of this cult of a divine mushroom, which we have found a revelation, in the true meaning of that abused word, but which for the Indians is an every-day feature, albeit a Holy Mystery, of their lives.

Here let me say a word parenthetically about the nature of the psychic disturbance that the eating of the mushroom causes. This disturbance is wholly different from the effects of alcohol, as different as night from day. We are entering upon a discussion where the vocabulary of the English language, of any European language, is seriously deficient. There are no apt words in them to characterize your state when you are, shall we say, 'bemushroomed.' For hundreds, even thousands, of years we have thought about these things in terms of alcohol, and we now have to break the bonds imposed on us by the alcoholic association. We are all, willy nilly, confined within the prison walls of our every-day vocabulary. With skill in our choice of words we may stretch accepted meanings to cover slightly new feelings and thoughts, but when a state of mind is utterly distinct, wholly novel, then all our old words fail. How do you tell a man born blind what seeing is like? In the present case, this is especially true because superficially the bemushroomed man shows a few of the objective symptoms of one intoxicated, drunk. Now virtually all the words describing the state of drunkenness, from 'intoxicated' (which, as you know, means 'poisoned') through the scores of

*This was on the night of June 29–30, 1955.

current vulgarisms, are contemptuous, belittling, pejorative. How curious it is that modern civilized man finds surcease from care in a drug for which he seems to have no respect! If we use by analogy the terms suitable for alcohol, we prejudice the mushroom, and since there are few among us who have been bemushroomed, there is danger that the experience will not be fairly judged. What we need is a vocabulary to describe all the modalities of a Divine Inebriant.

These difficulties in communicating have played their part in certain amusing situations. Two psychiatrists who have taken the mushroom and known the experience in its full dimensions have been criticised in professional circles as being no longer 'objective.' Thus it comes about that we are all divided into two classes: those who have taken the mushroom and are disqualified by our subjective experience, and those who have not taken the mushroom and are disqualified by their total ignorance of the subject! As for me, a simple layman, I am profoundly grateful to my Indian friends for having initiated me into the tremendous Mystery of the mushroom. In describing what happens, I shall be using familiar phrases that may seem to give you some idea of the bemushroomed state. Let me hasten to warn you that I am painfully aware of the inadequacy of my words, any words, to conjure up for you an image of that state.

I shall take you now to the monolingual villages in the uplands of southern Mexico. Only a handful of the inhabitants have learned Spanish. The men are appallingly given to the abuse of alcohol, but in their minds the mushrooms are utterly different, not in degree, but in kind. Of alcohol they speak with the same jocular vulgarity that we do. But about mushrooms they prefer not to speak at all, at least when they are in company and especially when strangers, white strangers, are present.

If you are wise, you will talk about something, anything, else. Then, when evening and darkness come and you are alone with a wise old man or woman whose confidence you have won, by the light of a candle held in the hand and talking in a whisper, you may bring up the subject. Now you will learn how the mushrooms are gathered, perhaps before sunrise, when the mountain side is caressed by the pre-dawn breeze, at the time of the New Moon, in certain regions only by a virgin. The mushrooms are wrapped in a leaf, perhaps a banana leaf, sheltered thus from irreverent eyes, and in some villages they are taken first to the church, where they remain for some time on the altar, in a *jícara* or gourd bowl. They are never exposed in the market-place but pass from hand to hand by prearrangement. I could talk to you a long time about the words used to designate these sacred mushrooms in the languages of the various peoples that know them. The Aztecs before the Spaniards arrived called them *teo-nanácatl*, God's flesh. I need hardly remind you of a disquieting parallel, the designation of the Elements in our Eucharist: 'Take, eat, this is my Body. . . .'; and again, 'Grant us therefore, gracious Lord, so to eat the flesh of thy dear son. . . .' But there is one difference. The orthodox Christian must accept by faith the miracle of the conversion of the bread into God's flesh: that is what is meant by the Doctrine of Transubstantiation. By contrast, the mushroom of the Aztecs carries its own conviction; every communicant will testify to the miracle that he has experienced. In the language of the Mazatecs, the sacred mushrooms are called *'nti*[1] *šǐ*[3]*tho*[3]. The first word, *'nti*[1], is a particle expressing reverence and endearment.* The second element means 'that which springs forth.' In 1953 our muleteer

* The superscript digits indicate the pitch of the syllable, [1] being the highest of four. The initial apostrophe indicates a glottal stop.

had travelled the mountain trails all his life and knew Spanish, though he could neither read nor write, nor even tell time by a clock's face. We asked him why the mushrooms were called 'that which springs forth.' His answer, breathtaking in its sincerity and feeling, was filled with the poetry of religion, and I quote it word for word as he gave it:

> El honguillo viene por sí mismo, no se sabe de dónde,
> como el viento que viene sin saber de dónde ni porqué.
>
> The little mushroom comes of itself, no one knows whence,
> like the wind that comes we know not whence nor why.

When we first went down to Mexico, we felt certain, my wife and I, that we were on the trail of an ancient and holy mystery, and we went as pilgrims seeking the Grail. To this attitude of ours I attribute such success as we have had. It has not been easy. For four and a half centuries the rulers of Mexico, men of Spanish blood or at least of Spanish culture, have never entered sympathetically into the ways of the Indians, and the Church regarded the sacred mushroom as an idolatry. The Protestant missionaries of today are naturally intent on teaching the Gospel, not on absorbing the religion of the Indians. Nor are most anthropologists good at this sort of thing... For more than four centuries the Indians have kept the divine mushroom close to their hearts, sheltered from desecration by white men, a precious secret. We know that today there are many *curanderos* who carry on the cult, each according to his lights, some of them consummate artists, performing the ancient liturgy in remote huts before minuscule congregations. With the passing years they will die off, and, as the country opens up, the cult is destined to disappear. They are hard to reach, these *curanderos*. Almost invariably they speak no Spanish. To them, performing before strangers seems a profanation. They will refuse even to meet with you, much

less discuss the beliefs that go with the mushrooms and perform for you. Do not think that it is a question of money: *no hicimos esto por dinero*, 'We did not this for money,' said Guadalupe, after we had spent the night with her family and the *curandera* María Sabina. Perhaps you will learn the names of a number of renowned *curanderos*, and your emissaries will even promise to deliver them to you, but then you wait and wait and they never come. You will brush past them in the marketplace, and they will know you, but you will not know them. The judge in the town-hall may be the very man you are seeking; and you may pass the time of day with him, yet never learn that he is your *curandero*.

After all, would you have it any different? What priest of the Catholic Church will perform Mass to satisfy an unbeliever's curiosity? The *curandero* who today, for a big fee, will perform the mushroom rite for any stranger is a prostitute and a faker, and his insincere performance has the validity of a rite put on by an unfrocked priest. In the modern world religion is often an etiolated thing, a social activity with mild ethical rules. Religion in primitive society was an awesome reality, 'terrible' in the original meaning of that abused word, pervading all life and culminating in ceremonies that were forbidden to the profane. This is what the mushroom ceremony is in the remote parts of Mexico.

We often think of the mysteries of antiquity as a manifestation of primitive religion. Let me now draw your attention to certain parallels between our Mexican rite and the Mystery performed at Eleusis. The timing seems significant. In the Mazatec country the preferred season for 'consulting the mushroom' is during the rains, when the mushrooms grow, from June through August. The Eleusinian Mystery was celebrated in September or early October, the season of the mushrooms in the Mediter-

ranean basin. At the heart of the Mystery of Eleusis lay a secret. In the surviving texts there are numerous references to the secret, but in none is it revealed. Yet Mysteries such as this one at Eleusis played a major rôle in Greek civilization, and thousands must have possessed the key. From the writings of the Greeks, from a fresco in Pompeii, we know that the initiate drank a potion. Then, in the depths of the night, he beheld a great vision, and the next day he was still so awestruck that he felt he would never be the same man as before. What the initiate experienced was 'new, astonishing, inaccessible to rational cognition.'* One writer in the 2nd century A.D., by name Aristides, pulled the curtain aside for an instant, with this fragmentary description of the Eleusinian Mystery:

> Eleusis is a shrine common to the whole earth, and of all the divine things that exist among men, it is both the most awesome and the most luminous. At what place in the world have more miraculous tidings been sung, where have the dromena called forth greater emotion, *where has there been greater rivalry between seeing and hearing?* And then he went on to speak of the 'ineffable visions' that it had been the privilege of many generations of fortunate men and women to behold.

Just dwell for a moment on that description. How striking that the Mystery of antiquity and our mushroom rite in Mexico are accompanied in the two societies by veils of reticence that, so far as we can tell, match each other point for point! Our ancient writers' words are as applicable to contemporary Mexico as they were to classic Greece! May it not be significant that the Greeks were wont to refer to mushrooms as 'the food of the gods,' *brōma theon*, and that Porphyrius is quoted as having

*For this and the following quotations see Walter F. Otto: The Meaning of the Eleusinian Mysteries, published in *The Mysteries*, 1955, ed. by Joseph Campbell, Pantheon Books, Bollingen Series XXX, 2; pp. 20 et seq. Italics are mine.

called them 'nurslings of the gods,' *theotróphos**? The Greeks of the classic period were mycophobes. Was this because their ancestors had felt that the whole fungal tribe was infected 'by attraction' with the holiness of some mushrooms and that they were not for mortal men to eat, at least not every day? Are we dealing with what was in origin a religious tabu?

In earliest times the Greeks confined the common European word for mushroom, which in their language was *sp(h)óngos* or *sp(h)óngê*, to the meaning 'sponge,' and replaced it by a special word, *múkês*, for the designation of mushrooms.‡ Now it happens that the root of this word *múkês* in Greek is a homonym of the root of the Greek word for 'Mystery,' *mu*. A bold speculation flashes through the mind. The word for 'Mystery' comes from a root that means the closing of the apertures of the body, the closing of the eyes and ears. If the mushroom played a vital and secret rôle in primitive Greek religion, what could be more natural than that the standard word for 'mushroom' would fall into disuse through a religious tabu (as in Hebrew 'Yahweh' gave way to 'Adonai') and

* Giambattista della Porta: *Villa*, 1592, Frankfort, p. 764.

‡ Holger Pedersen in an early paper contended that the basic fungal words of Europe were identical: Old High German *swamb*, Slavic *gomba*, Lithuanian *gumbas*, Latin *fungus*, Greek *sp(h)óngos*, *sp(h)óngê*, and Armenian *sung*, *sunk*. (Published in Polish: 'Przyczynki do gramatyki porównawczej jezyków slowianskich,' in *Materyaly i Prace Komisyi Jezykowej Akademii Umieietnosci w Krakowie*, Cracow, 1(1): 167–176.) Since then some philologists have declined to accept this thesis as more than a possibility, especially as to the Slavic term, but Professor Roman Jakobsan in a recent personal communication to me says: 'The etymology of Holger Pedersen, the great Danish specialist in the comparative study of Indo-European languages, seems to me and to many other linguists, e.g., the distinguished Czech etymologist V. Machek, as the only convincing attempt to interpret the fungal name of the European languages. Not one single serious argument has been brought againt Pedersen's "attractive" explanation, as Berneker defines it, and not one single defensible hypothesis has been brought to replace this one.'

that the Greeks substituted an alternative fungal term that was a homonym of 'mystery'? You can hear the pun, see the gesture, 'Mum's the word,' with the index finger over the mouth. . . . We must remember, in considering this problem, that in antiquity the ecology of Greece and the Greek isles was different from now. Deforestation and the goats had not wrought the havoc of the intervening centuries. They had not left the mountains naked to the sun. On the wooded isles and in the forests of the mainland, there must have been a wealth of mushrooms.

Let us consider possibilities other than the mushroom. In the Mazatec country the Indians, when there are no mushrooms, have recourse to alternatives. Thanks to the brilliant work of Dr. Albert Hofmann of Sandoz, the Swiss pharmaceutical firm, we are now sorting out and identifying a whole series of indoles that have remarkable psychotropic properties. As you all know, he has isolated the active agents in some of our Mexican mushrooms, psilocybin and psilocin, two tryptamine derivatives and members of the indole family of substances. He has defined their molecular structure. The magic indoles are present in other plants used widely among the Indians of Mexico. With Dr. Hofmann's permission, I am able to announce to you tonight that, only in July of this year, he has isolated and identified three of the active agents in *ololiuqui*, the famous seeds, subject of many studies, that have long been used in Mexico for their psychotropic properties.* In the Mazatec country the seeds of *ololiuqui* are one of the alternatives used when the sacred mushrooms are not available. Imagine our surprise, when we began looking for these seeds in quantity last year, to discover that the Zapotec Indians, em-

* The Chemistry of Natural Products, paper read by Dr. Hofmann, Aug. 18, 1960, in the I.U.P.A.C. Symposium, Melbourne.

ploy two seeds: in some villages one, in others the other, and in some both. There is no question which seed was the *ololiuqui* of the Aztecs. It is a climbing morning-glory known to science as *Rivea corymbosa* (L.) Hallier filius.* The seeds are brown and almost round. The second plant was identified at the National Herbarium in Washington as *Ipomoea violacea* L.,‡ also a climbing morning-glory but easily distinguished in the field from *Rivea corymbosa*. The seeds are long, black, and angular, and so far as we now know, they are used only in some parts of the Zapotec country. Both are called in Zapotec *badoh*, but the black seeds are *badoh negro*, black *badoh*, to distinguish them from the true *ololiuqui* seeds.°

*The best summary of the *ololiuqui* literature and problem is Richard Evans Schultes' A Contribution to Our Knowledge of *Rivea corymbosa*, the Narcotic Ololiuqui of the Aztecs, Botanical Museum, Harvard University, 1941. Also see Humphrey Osmond's Ololiuqui: The Ancient Aztec Narcotic, *Journal of Mental Science*, July 1955, 101 (424): 526–537. Dr. Osmond reports on the effects of the seeds on himself.

‡**Ipomoea violacea** *Linnaeus* Pl. Sp. (1953) 161.
Convolvulus indicus Miller Gard. Dict. (1768) No. 5.
Ipomoea tricolor Cavanilles Icon. Pl. Rar. 3 (1794) 5.
Convolvulus violaceus Sprengel Syst. 1 (1825) 399.
Convolvulus venustus Sprengel Syst. 1 (1825) 399.
Ipomoea rubrocoerulea Hooker Bot. Mag. (1834) t. 3297.
Pharbitis violacea (L.) Bojer Hort. Maurit. (1837) 227.
Tereietra violacea (L.) Rafinesque Fl. Tellur. 4 (1839) 124.
Ipomoea Hookeri G. Don Gen. Syst. 4 (1838) 274.
Pharbitis rubrocoeruleus (Hook.) Planchon Fl. des Serres 9 (1854) 281.
Convolvulus rubrocoeruleus (Hook.) D. Dietrich Syn. Pl. 1 (1839) 670.
Ipomoea puncticulata Bentham Bot. Voy. Sulph. (1945) 136.

° Credit for the discovery of the ceremonial use of *Ipomoea violacea* seeds goes to Thomas MacDougall and Francisco Ortega ('Chico'), famous Zapotec guide and itinerant trader. They have not yet delimited the area of diffusion, but they have found *badoh negro* seeds in use in the following Zapotec towns and villages in the uplands of southern Oaxaca: San Bartolo Yautepec, San Carlos Yautepec and Santa Catarina Quieri, all in the district of Yautepec; Santa Cruz

Dr. Hofmann found that the alkaloidal components of the two seeds were identical, and they yielded d-lysergic acid amide and d-isolysergic acid amide, in the LSD 25 family of substances and known heretofore only as derivatives of ergot. Is it not surprising to find in higher plants such as the Convolvulaceae the same lysergic acid derivatives as in the lower fungi? The third substance found in these seeds was *chanoclavine*, also isolated by Dr. Hofmann et al. some years ago from a culture of *Claviceps* species.*

Thus it comes about that, thanks to the achievements of our biological chemists, we may be on the brink of rediscovering what was common knowledge among the ancient Greeks. I predict that the secret of the Mysteries will be found in the indoles, whether derived from mushrooms or from higher plants or, as in Mexico, from both.

I would not be understood as contending that only these substances (wherever found in nature) bring about visions and ecstasy. Clearly some poets and prophets and many mystics and ascetics seem to have enjoyed ecstatic visions that answer the requirements of the ancient Mysteries and that duplicate the mushroom agapé of Mexico. I do not suggest that St. John of Patmos ate mushrooms in order to write the Book of the Revelation. Yet the succession of images in his Vision, so clearly seen and yet

---

Ozolotepec and San Andrés Lovene, District of Miahuatlan; and finally a settlement called Roalo, between Zaachila and Zimatlan, just south of the city of Oaxaca. In San Bartolo *I. violacea* is used to the exclusion of *Rivea corymbosa*, but in the other towns both are used. These data are based on personal correspondence and also Thomas MacDougall: *Ipomoea tricolor:* A Hallucinogenic Plant of the Zapotecs, in *Boletín* of the Centro de Investigaciones Antropológicas de México, No. 6, March 1, 1960. Reports from Juquila, to the west of the Zapotec towns mentioned above, indicate that *I. violacea* seeds may also be used among the Chatino Indians.

* A. Hofmann with R. Brunner, H. Kobel, and A. Brack, *Helv. Chem. Acta*, 1957, 40: 1358.

such a phantasmagoria, means for me that he was in the same state as one bemushroomed. Nor do I suggest for a moment that William Blake knew the mushroom when he wrote this telling account of the clarity of 'vision':

> The Prophets describe what they saw in Vision as real and existing men, whom they saw with their imaginative and immortal organs; the Apostles the same; the clearer the organ the more distinct the object. A Spirit and a Vision are not, as the modern philosophy supposes, a cloudy vapour, or a nothing: they are organized and minutely articulated beyond all that the mortal and perishing nature can produce. *He who does not imagine in stronger and better lineaments, and in stronger and better light than his perishing eye can see, does not imagine at all.* [Italics mine. From *The Writings of William Blake*, ed. by Geoffrey Keynes, vol. III, p. 108]

This must sound cryptic to one who does not share Blake's vision or who has not taken the mushroom. The advantage of the mushroom is that it puts many (if not everyone) within reach of this state without having to suffer the mortifications of Blake and St. John. It permits you to see, more clearly than our perishing mortal eye can see, vistas beyond the horizons of this life, to travel backwards and forwards in time, to enter other planes of existence, even (as the Indians say) to know God. It is hardly surprising that your emotions are profoundly affected, and you feel that an indissoluble bond unites you with the others who have shared with you in the sacred agapé. All that you see during this night has a pristine quality: the landscape, the edifices, the carvings, the animals—they look as though they had come straight from the Maker's workshop. This newness of everything—it is as though the world had just dawned—overwhelms you and melts you with its beauty. Not unnaturally, what is happening to you seems to you freighted with significance, beside which the humdrum events of everyday are trivial. All these things you see with an immediacy of vision that leads you to say to

yourself, 'Now I am seeing for the first time, seeing direct, without the intervention of mortal eyes.' (Plato tells us that beyond this ephemeral and imperfect existence here below, there is another Ideal world of Archetypes, where the original, the true, the beautiful Pattern of things exists for evermore. Poets and philosophers for millenniums have pondered and discussed his conception. It is clear to me where Plato found his Ideas; it was clear to his contemporaries too. Plato had drunk of the potion in the Temple of Eleusis and had spent the night seeing the great Vision.)

And all the time that you are seeing these things, the priestess sings, not loud, but with authority. The Indians are notoriously not given to displays of inner feelings—except on these occasions. The singing is good, but under the influence of the mushroom you think it is infinitely tender and sweet. It is as though you were hearing it with your mind's ear, purged of all dross. You are lying on a *petate* or mat; perhaps, if you have been wise, on an air mattress and in a sleeping bag. It is dark, for all lights have been extinguished save a few embers among the stones on the floor and the incense in a sherd. It is still, for the thatched hut is apt to be some distance away from the village. In the darkness and stillness, that voice hovers through the hut, coming now from beyond your feet, now at your very ear, now distant, now actually underneath you, with strange ventriloquistic effect. The mushrooms produce this illusion also. Everyone experiences it, just as do the tribesmen of Siberia who have eaten of *Amanita muscaria* and lie under the spell of their shamans, displaying as these do their astonishing dexterity with ventriloquistic drum-beats. Likewise, in Mexico, I have heard a shaman engage in a most complicated percussive beat: with her hands she hits her chest, her thighs, her forehead, her arms, each giving a

different resonance, keeping a complicated rhythm and modulating, even syncopating, the strokes. Your body lies in the darkness, heavy as lead, but your spirit seems to soar and leave the hut, and with the speed of thought to travel where it listeth, in time and space, accompanied by the shaman's singing and by the ejaculations of her percussive chant. What you are seeing and what you are hearing appear as one: the music assumes harmonious shapes, giving visual form to its harmonies, and what you are seeing takes on the modalities of music—the music of the spheres. 'Where has there been greater rivalry between seeing and hearing?' How apposite to the Mexican experience was the ancient Greek's rhetorical question! All your senses are similarly affected: the cigarette with which you occasionally break the tension of the night smells as no cigarette before had ever smelled; the glass of simple water is infinitely better than champagne. Elsewhere I once wrote that the bemushroomed person is poised in space, a disembodied eye, invisible, incorporeal, seeing but not seen. In truth, he is the five senses disembodied, all of them keyed to the height of sensitivity and awareness, all of them blending into one another most strangely, until the person, utterly passive, becomes a pure receptor, infinitely delicate, of sensations. (You, being a stranger, are perforce only a receptor. But the Mazatec communicants are also participants with the *curandera* in an extempore religious colloquy. Her utterances elicit spontaneous responses from them, responses that maintain a perfect harmony with her and with each other, building up to a quiet swaying antiphonal chant. In a successful ceremony this is an essential element, and one cannot experience the full effect of the rôle of the mushroom in the Indian community unless one attends such a gathering, either alone or with one or at most two other strangers.) As your body lies there in its sleep-

ing bag, your soul is free, loses all sense of time, alert as it never was before, living an eternity in a night, seeing infinity in a grain of sand. What you have seen and heard is cut as with a burin in your memory, never to be effaced. At last you know what the ineffable is, and what ecstasy means. Ecstasy! The mind harks back to the origin of that word. For the Greeks *ekstasis* meant the flight of the soul from the body. Can you find a better word than that to describe the bemushroomed state? In common parlance, among the many who have not experienced ecstasy, ecstasy is fun, and I am frequently asked why I do not reach for mushrooms every night. But ecstasy is not fun. Your very soul is seized and shaken until it tingles. After all, who will choose to feel undiluted awe, or to float through that door yonder into the Divine Presence? The unknowing vulgar abuse the word, and we must recapture its full and terrifying sense. . . . A few hours later, the next morning, you are fit to go to work. But how unimportant work seems to you, by comparison with the portentous happenings of that night! If you can, you prefer to stay close to the house, and, with those who lived through that night, compare notes, and utter ejaculations of amazement.

As man emerged from his brutish past, thousands of years ago, there was a stage in the evolution of his awareness when the discovery of a mushroom (or was it a higher plant?) with miraculous properties was a revelation to him, a veritable detonator to his soul, arousing in him sentiments of awe and reverence, and gentleness and love, to the highest pitch of which mankind is capable, all those sentiments and virtues that mankind has ever since regarded as the highest attribute of his kind. It made him see what this perishing mortal eye cannot see. How right the Greeks were to hedge about this Mystery, this imbibing of the potion, with secrecy and surveil-

lance! What today is resolved into a mere drug, a tryptamine or lysergic acid derivative, was for him a prodigious miracle, inspiring in him poetry and philosophy and religion. Perhaps with all our modern knowledge we do not need the divine mushrooms any more. Or do we need them more than ever? Some are shocked that the key even to religion might be reduced to a mere drug. On the other hand, the drug is as mysterious as it ever was: 'like the wind it cometh we know not whence, nor why.' Out of a mere drug comes the ineffable, comes ecstasy. It is not the only instance in the history of humankind where the lowly has given birth to the divine. Altering a sacred text, we would say that this paradox is a hard saying, yet one worthy of all men to be believed.

If our classical scholars were given the opportunity to attend the rite at Eleusis, to talk with the priestess, what would they not exchange for that chance? They would approach the precincts, enter the hallowed chamber, with the reverence born of the texts venerated by scholars for millenia. How propitious would their frame of mind be, if they were invited to partake of the potion! Well, those rites take place now, unbeknownst to the classical scholars, in scattered dwellings, humble, thatched, without windows, far from the beaten track, high in the mountains of Mexico, in the stillness of the night, broken only by the distant barking of a dog or the braying of an ass. Or, since we are in the rainy season, perhaps the Mystery is accompanied by torrential rains and punctuated by terrifying thunderbolts. Then, indeed, as you lie there bemushroomed, listening to the music and seeing the visions, you know a soul shattering experience, recalling as you do the belief of some primitive peoples that mushrooms, the sacred mushrooms, are divinely engendered by Jupiter Fulminans, the God of the Lightning-bolt, in the Soft Mother Earth.

Appendix

The following enumeration is the first list published in English of the hallucinogenic mushrooms of Mexico. With each name we give the place of publication of (1) the technical name of the mushroom and (2) the earliest report of its use in Mexico as a divinatory agent. Doubtless more species will be discovered, but we believe our list is complete through 1960.

Not all divinatory mushrooms are hallucinogenic. The Indians consume some kinds for divinatory purposes because of their suggestive shape. This is true of *Cordyceps capitata* (Holmsk.) Link, as well as its host fungi, *Elaphomyces granulatus* Fr. or *Elaphomyces variegatus* Vitt., and also of *Dictyophora phalloidea* Desvaux. *Cordyceps capitata* has been found to contain an indolic compound that might cause hallucinations, but only in trace amounts. There are also reports of the use of *Clavaria truncata* Quél. and *Nevrophyllum floccosum* (Schw.) Heim, but their hallucinogenic virtue remains doubtful, and they are always taken in conjunction with *Psilocybe Wassonii* Heim. (See Les champ. halluc. du Mexique, 1958, pp. 81, 83, 99, 162.) *Psilocybe muliercula* Singer & Smith has been reported as an hallucinogen (in Mycologia 50 (1958) 145), but this concept is a synonym of *Ps. Wassonii* (see below).

Professor Roger Heim and I accept responsibility for all species and varieties listed that are marked by an asterisk.

***Conocybe siligineoides** *Heim* in Rev. Mycol. 22 (1957) 197.

Use first reported: in Comptes Rend. 242 (1956) 1391.

Panaeolus fimicola (*Fr.*) *Quélet ex Fries* Hym. Europ. (1874) 312.
Use first reported: in Bol. Soc. Bot. Mex. No. 24 (1959) 23.

Panaeolus sphinctrinus (*Fr.*) *Quélet ex Fries* Epicr. syst. mycol. seu synops. Hymenomyc. (1836–38) 235.
Use first reported: in Bot. Mus. Leafl. Harvard Univ. 7 (1939) 37 (as *P. campanulatus* L. var. *sphinctrinus* (Fr.) Bresadola).

Psathyrella sepulchralis *Singer, Smith & Guzmán* in Lloydia 21 (1958) 26.
Use first reported: loc. cit.

***Psilocybe acutissima** *Heim* in Rev. Mycol. 24 (1959) 106.
Use first reported: in Les champ. halluc. du Mexique (1958) 166.

***Psilocybe aztecorum** *Heim* in Rev. Mycol. 22 (1957) 78.
Use first reported: in Comptes Rend. 244 (1957) 699.

***Psilocybe caerulescens** *Murrill* var. **mazatecorum** *Heim* in Rev. Mycol. 22 (1957) 78.
Psilocybe mazatecorum Heim in Comptes Rend. 242 (1956) 1392, *nomen prov., sine diagn. lat.*
Use first reported: loc. cit.

***Psilocybe caerulescens** *Murrill* var. **mazatecorum** *Heim* fma. **heliophila** *Heim* in *Heim & Wasson* Les champs. halluc. du Mexique (1958) 141, *sine diagn. lat.*
Use first reported: loc. cit.

*Psilocybe caerulescens *Murrill* var. **mazatecorum** *Heim*. fma. **ombrophila** *Heim* in *Heim & Wasson* Les champs. halluc. du Mexique (1958) 140, *sine diagn. lat.*
Use first reported: loc. cit.

*Psilocybe caerulescens *Murrill* var. **nigripes** *Heim* in Rev. Mycol. 22 (1957) 79.
Use first reported: in Comptes Rend. 244 (1957) 698.

Psilocybe caerulipes (*Peck*) *Saccado* var. **Gastonii** *Singer & Smith* in Sydowia 12 (1959) 236.
Use first reported: loc. cit.

Psilocybe candidipes *Singer & Smith* in Mycologia 50 (1958) 141.
Use first reported: loc. cit. 250.

*Psilocybe cordispora *Heim* in Rev. Mycol. 24 (1959) 103.
Use first reported: in Comptes Rend. 242 (1956) 1390.

*Psilocybe fagicola *Heim & Cailleux* in Rev. Mycol. 24 (1959) 438.
Use first reported: in Comptes Rend. 249 (1959) 1843.

*Psilocybe Hoogshagenii *Heim* in Rev. Mycol. 24 (1959) 104.
Use first reported: in Les champs. halluc. du Mexique (1958) 167.

Psilocybe isauri *Singer* in Sydowia 12 (1959) 237.
Use first reported: loc. cit.

*Psilocybe mexicana *Heim* in Rev. Mycol. 22 (1957) 77.
Use first reported: in Comptes Rend. 242 (1956) 966.

*Psilocybe mixaeensis *Heim* in Rev. Mycol. 24 (1959) 104.
Use first reported: in Les champs. halluc. du Mexique (1958) 169.

*Psilocybe semperviva *Heim & Cailleux* in Rev. Mycol. 23 (1958) 352.
Use first reported: in Comptes Rend. 245 (1957) 1764.

*Psilocybe Wassonii *Heim* in Rev. Mycol. 23 (1958) 119.
Psilocybe mulicrcula Singer & Smith in Mycologia 50 (1958) 142.
Use first reported: in Comptes Rend. 245 (1957) 1763.

*Psilocybe yungensis *Singer & Smith* in Mycologia 50 (1958) 142.
Use first reported: in Bol. Soc. Mex. No. 24 (1959) 22.

*Psilocybe zapotecorum *Heim* in Rev. Mycol. 22 (1957) 77.
Use first reported; in Comptes Rend. 242 (1956) 1393.

*Psilocybe zapotecorum *Heim* var. elongata *Heim* in Comptes Rend. 250 (1960) 1158, *nomen prov., sine diagn. lat.*

*Stropharia cubensis *Earle* Inf. An. Establ. Centr. Agron. Cub. 1 (1906) 240.
Psilocybe cubensis (Earle) Singer in Lilloa 22 (1949) 507.
Use first reported: in Comptes Rend. 242 (1956) 967.

BOTANICAL MUSEUM LEAFLETS
HARVARD UNIVERSITY

CAMBRIDGE, MASSACHUSETTS, APRIL 11, 1961 VOL. 19, NO. 8

FURTHER ARCHAEOLOGICAL EVIDENCE ON THE EFFECTS OF TEOSINTE INTROGRESSION IN THE EVOLUTION OF MODERN MAIZE

BY

WALTON C. GALINAT AND REYNOLD J. RUPPÉ[1]

ANOTHER large and significant collection of prehistoric maize cobs (*Zea Mays* L.) with Tripsacoid characteristics that are indicative of introgression from either *Tripsacum* spp. or its maize derivative, teosinte[2] (*Zea mexicana* Reeves and Mangelsdorf), has been provided by the archaeologist, who is the junior author, for botanical analysis. Although there have been about a dozen other collections of prehistoric Tripsacoid cobs from northwestern Mexico and southwestern United States, the present material, which comes from Cebollita Cave in New Mexico, is the first large (2575 cobs), stratified (five levels) collection to become available for statistical treatment.

Our previous statistical study (Galinat, *et al.*, 1956) of Tripsacoid cobs involved a large non-stratified collection from two caves in Arizona. At that time we established

[1] Arizona State University, Tempe, Arizona.

[2] For the purposes of discussion and consistency, we shall assume, as we have previously, that the immediate source of the introgression represented by these archaeological specimens is from teosinte rather than from less likely hybridization with *Tripsacum*.

the reliability of scoring for teosinte introgression according to the degree of induration by showing that the more indurated archaeological cobs are like modern maize-teosinte derivatives in having a higher specific gravity which is also positively correlated, in modern maize, to number of teosinte chromosomes.

According to this system, induration is subjectively estimated with an arbitrary key of five grades. At grade-1 the glumes and rachis are non-indurated and somewhat flexible. At grade-5 the glumes and rachis are not only highly indurated, but the glumes are curved upwards and at least some pistillate spikelets are borne singly, features which are common in maize-teosinte hybrids, but absent in typical maize.

By applying this method to estimate teosinte introgression in the present stratified material, we may now determine the evolutionary effects of such introgression upon the maize from this site.

Description of the Site

The archaeological maize upon which this study is based was excavated from Cebollita Cave in the Cebolleta Mesa[1] area in Valencia County, New Mexico, about twenty miles south of the town of Grants. The area is bounded on the west by the McCarthys' Lava Flow and on the east by the western slope of Cebolleta Mesa. It is in the Upper Sonoran climatic zone at an elevation of about 7000 feet. The terrain consists of broad valley floors and sheer sandstone cliffs. The cave is located in a vertical sandstone cliff in the Zuni sandstone member. It faces south and opens out on a broad valley, which,

[1] According to the principal maps of the area, the name of the mesa is spelled Cebolleta while the name of the cave which contained the archaeological maize is spelled Cebollita. The latter spelling comes from the Spanish word meaning "little onion."

before channel cutting had commenced, must have been an ideal flood-farming area.

The flora includes piñon pine, juniper, manzanita (*Arctostaphyllos pungens*), sage, blue gramma grass, yucca, bee weed (*Cleome serrulata* Pursh), and several varieties of cacti. Canyon floors in the area normally have a good stand of blue gramma grass mixed with some cacti, yucca, sage brush, and manzanita. Minor depressions are covered by a thick stand of bee plants and sunflowers after the beginning of the rainy season. Scattered stands of juniper and piñon pine are found on the valley floors. Deer, coyotes, prairie dogs, rabbits, lizards, and snakes constitute most of the faunal assemblage.

The climate is semi-arid and precipitation averages about eleven inches annually. The growing season can only be estimated from reports of government stations near Cebolleta Mesa and is thought to be about 110 days long. It is assumed that the climate at the time the cave was inhabited was approximately the same as today.

The site is a fourteen room pueblo situated in Cebolita Cave. The pueblo was built piece-meal and abandoned at least once during its existence. The abundant rock fall from the roof attests to the hazards of life in the cave. An enormous block of sandstone fell from the roof at one time and caused a temporary abandonment of the pueblo. When the pueblo was reinhabited, it was by a group who had a slightly different culture than the previous occupants. Although the cave was inhabited in the Pre-pueblo and Pueblo I periods, the pueblo itself was not constructed until the end of the Pueblo II period. The entire occupation of the pueblo was encompassed within the Early Pueblo III period, from about 1050 to 1200 A.D. as dated by ceramic typology.

Preservation of organic material in the pueblo was variable due to run-off water from the mesa top which flowed

into some of the rooms. Those rooms which remained dry contained large amounts of vegetal remains such as corn, squash, and other seeds, together with cordage, matting, sandals, basketry, and wooden objects. Most of the corn utilized in the present study was found in Rooms B, C, and D in the back of the cave. Room B contained four feet of deposit, the deepest fill in the pueblo.

The archaeological value of the maize under discussion lies in the fact that the excellent stratigraphic evidence indicates an interesting history of human occupation in the pueblo. Room B supplied most of the evidence and most of the maize. Level 5 in Room B marks the earliest occupation of the pueblo. Three hard-packed adobe floors were superimposed at the base of this level. The original maize at the site was found on the uppermost floor and occurred in fifteen concentrations of charred, shelled kernels, ashes, and heat-warped pot sherds. More than 500 charred ears were also found lying on the floor. The concentrations of shelled kernels had been stored in pots and the loose ears must have been hung from the roof beams.

All of the material found in Level 5 and the lower half of Level 4 was burned. A three-foot thick concentration of spalled sandstone slabs was found above Level 5 and the lower half of Level 4. The slabs had spalled off the cave ceiling as a result of the fire that destroyed Room B. In addition, a huge block of sandstone weighing many tons fell across Rooms D and E. The fire and rock fall terminated occupation of the site for a time, but, pending study of the dendrochronological specimens, the duration of the abandonment is unknown.

The Ceramic Assemblage

Reoccupation of the pueblo was accomplished by a group of Indians using a slightly later variant of the Early Pueblo III ceramic types (normal Tularosa phase)

than their predecessors. Greater changes in the type of pottery than those observed would be expected if the period of abandonment had been long. A quarter of the total number of sherds from one room occupied by the newcomers was of the brown paste type, an atypical proportion for the area at that time, but the other rooms do not show as high a proportion.

Perishable Material other than Maize

A large amount of perishable material other than maize was found in the upper levels, including nine sandals, five wooden arrow foreshafts, a number of fragments of basketry and matting and several hundred pieces of plain, fur, or feather-wrapped cordage. One of the sandals is a modified fish-tail type of the kind found throughout the Mogollon area (Cosgrove, 1947, fig. 92-9b; Haury, 1934, plate 41; Bluhm, 1952, p. 271). It is interesting to note in this connection that Cosgrove also found Tripsacoid maize together with this type of sandal in the Hueco Mountain caves. Two of the other sandals were typical of the Four Corners Region in Basketmaker and Pueblo III horizons (Kidder and Guernsey, 1919). A similar type was also found at Bat Cave (Herbert Dick, unpub.) and in Tularosa Cave (Bluhm, 1952, p. 279).

The sandals might suggest that the newcomers originated from somewhere in the Mogollon region, but such a conclusion is based on slim evidence at best. Recent researches in the Cebolleta Mesa area have resulted in the conclusion that there is a region of cultural blending between the Anasazi and Mogollon regions. In this case, since the Cebolleta Mesa area is on the southern periphery of the Anasazi region, it might have received influences from the blend region just to its south. Therefore, it seems likely that the possessors of the Tripsacoid maize may have come from this blend region.

Level 5 Maize

The maize ears from the lowest stratum (Level 5), resemble those of the race "Chapalote," an ancient indigenous race of Mexico described by Wellhausen *et al.*, 1952, and the principal, if not the only race of the early cultures from this part of North America (Mangelsdorf and Lister, 1956). At Bat Cave, New Mexico, a primitive form of Chapalote remaining from an incipient cultivation tradition dates back to between 3500 and 2500 B.C. (Mangelsdorf, 1954). Some of the prehistoric maize from coastal Peru (about 600 B.C.) may also have affinities with Chapalote (Grobman and Mangelsdorf, 1959).

Identification of the original Cebollita maize as Chapalote was possible because most of the ears were perfectly preserved by a carbonization process resulting from incomplete combustion. The original Cebollita maize and Chapalote share the following characteristics. Their ears are cigar shaped, with a slight tapering at both base and tip. Prominent glumes may protrude between the kernels. Small, hard kernels are rounded on top and nearly isodiametric in length, width, and thickness. The vertical rows of these kernels, especially those of 10- and 14-rowed ears, have a strong tendency to twist. A relatively high row number in combination with a slender rachis. forces the cupule wings and paired kernels to interlock[1] slightly with the lateral rows on either side. The interlocking of cupule wings creates the illusion of broad cupules. The actual cupule width (5.5 mm.) is like the kernel width (6.0 mm.) in being only about one-half that of other North American races such as the 8-rowed flour and flint types.

A comparison of the actual values in Cebollita maize

[1] Interlocking of adjacent pairs of kernels, sometimes called tessellation, is also found in a primitive Peruvian race, Confite Morocho, and certain of its derivatives (Grobman, unpub.).

with those of modern Chapalote from the Mexican states of Sonora and Sinaloa and with those of certain early Basket Maker ears (about 800 A.D.) obtained from the studies of Hurst and Anderson (1949) on maize from Cottonwood Cave, Colorado, reveals that the ears from Cebollita Cave are slightly smaller (Table I). The date of the Cebollita maize (about 1050 A.D.) seems to exclude it as a more primitive or inherently smaller type of Chapalote. Rather, reduction may be a depauperate condition resulting from poor growing conditions. The latter suggestion is supported by the fact that the best Level 5 ears compare favorably to those of modern Chapalote and Cottonwood Cave maize.

The termination of Level 5 was marked by a fire which either carbonized or charred all of the original Chapalote cobs and caused a large rock fall from the ceiling, as well as a temporary abandonment of the cave.

Level 4 Maize

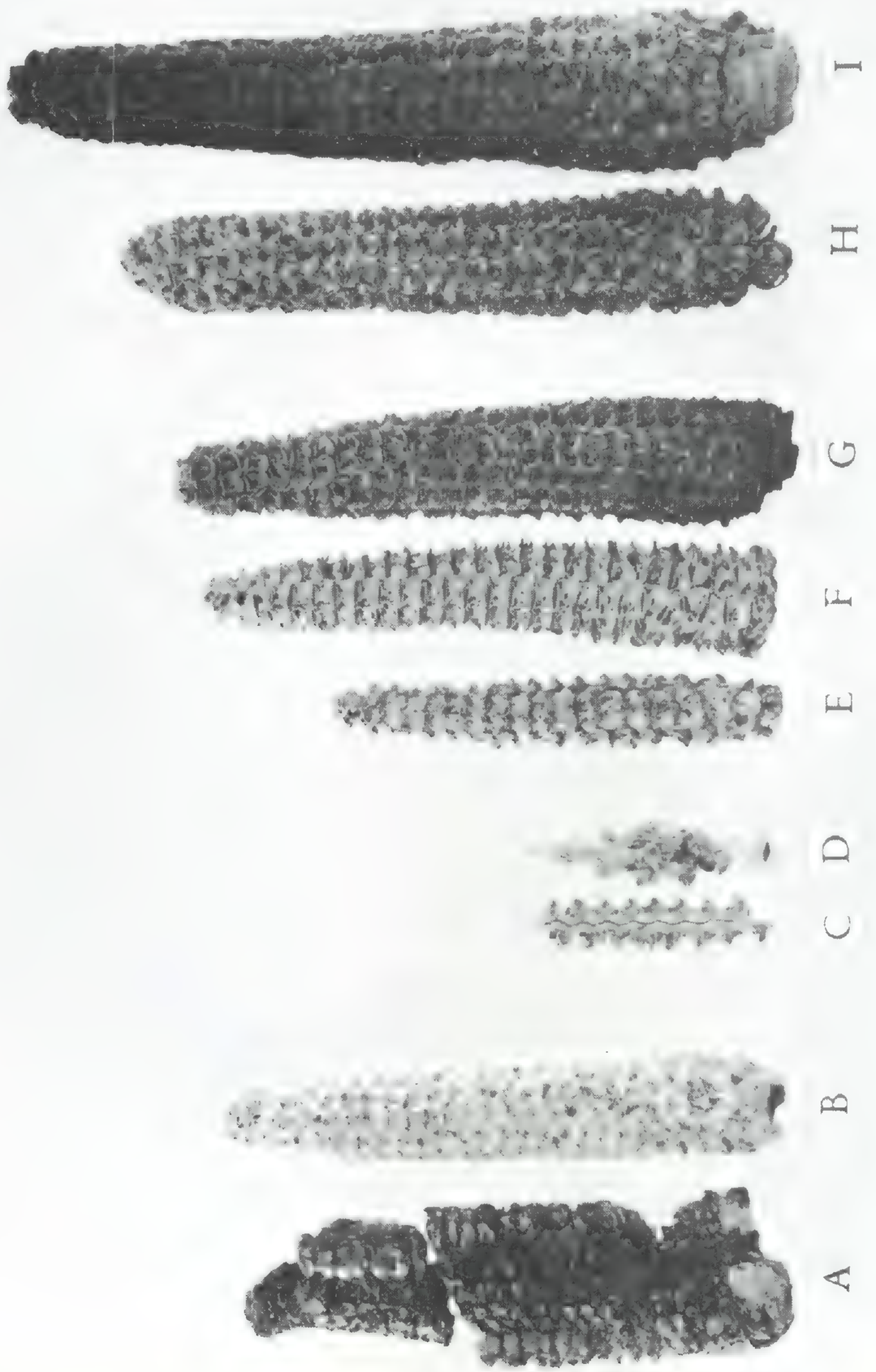
Upon reoccupation of the cave, as designated by Level 4, 85% of the cobs changed abruptly to the Tripsacoid type of maize which was becoming widespread throughout southwestern United States during this period (1000–1200 A.D.). Three percent of these were almost exact counterparts of modern F_1 hybrids or hybrid segregates from experimental crosses between maize and teosinte in being two-ranked for at least part of their length, and in having highly indurated, upward-curved glumes (Plate XXIII, cobs C, D). Such highly Tripsacoid cobs were scored as grade-5 according to our system of estimating the degree of teosinte introgression with an arbitrary key of five grades. On the average, the Level 4 specimens were the most Tripsacoid from the entire site, having an average introgression grade of 2.6.

At the other extreme, fifteen percent of the Level 4

EXPLANATION OF THE ILLUSTRATION

PLATE XXIII. A series of cobs from the various levels in Cebollita Cave. The original Chapalote maize (cob A) of Level 5 has some non-carbonized counterparts (cob B) in Level 4. Note the soft glumes of cob B. Level 4 also contains many small highly Tripsacoid cobs (C, D) similar to segregates of experimental hybrids between maize and teosinte. Although Level 3 (cobs E, F, G) marks the beginning of a progressive decrease in the indurative effects of the teosinte introgression, the variability which it had introduced continues to increase. Finally in Levels 2 and 1, there is almost complete recovery from the detrimental effects of the introgression and many of the cobs (H, I) are larger and probably more productive than the original Chapalote maize. About one half natural size.

PLATE XXIII



cobs were scored as grade-1, because they had long soft glumes which were structurally similar to the carbonized ones from the original Chapalote in the previous level. Some of the soft-glumed cobs were also identical in all other characteristics to the original specimens except in being non-carbonized. Therefore, the continuity of the population of cobs was not completely broken by the change to Tripsacoid maize.

The sudden change to these Tripsacoid cobs of Level 4 does not preclude a change in maize background from that of the original Chapalote. Teosinte introgression had already occurred much earlier in the Chapalote from other parts of New Mexico (Bat Cave in Catron County, Mangelsdorf and Smith, 1949); it was well established in this race in northwestern Mexico by 750±250 A.D. (Mangelsdorf and Lister, 1956). Inasmuch as Tripsacoid Chapalote was prevalent then and there is no evidence in type of ceramics or sandals of trade from far outside the area, the new variation is attributed to teosinte introgression in Chapalote.

The onset of teosinte introgression caused a marked drop in the average size of cob to the lowest values for the site. The average kernel row-number dropped by 11%, the cob diameter by 10%, and the cob length by 22% below that of the original Chapalote. These reductions represent modification toward the spike of teosinte and are correlated to estimated teosinte introgression in the population as a whole (Plate XXIV, figs. 1, 2, 3).

These reductions in average cob size in the Tripsacoid maize may not reflect a corresponding loss in over-all yield per plant or per acre of plants. Some modern maize breeders have found that a reduction in ear size in teosinte derivatives of maize tends to be compensated for by an increase in number of ears per plant. However, some of the energy in Tripsacoid maize may be diverted away

PLATE XXIV

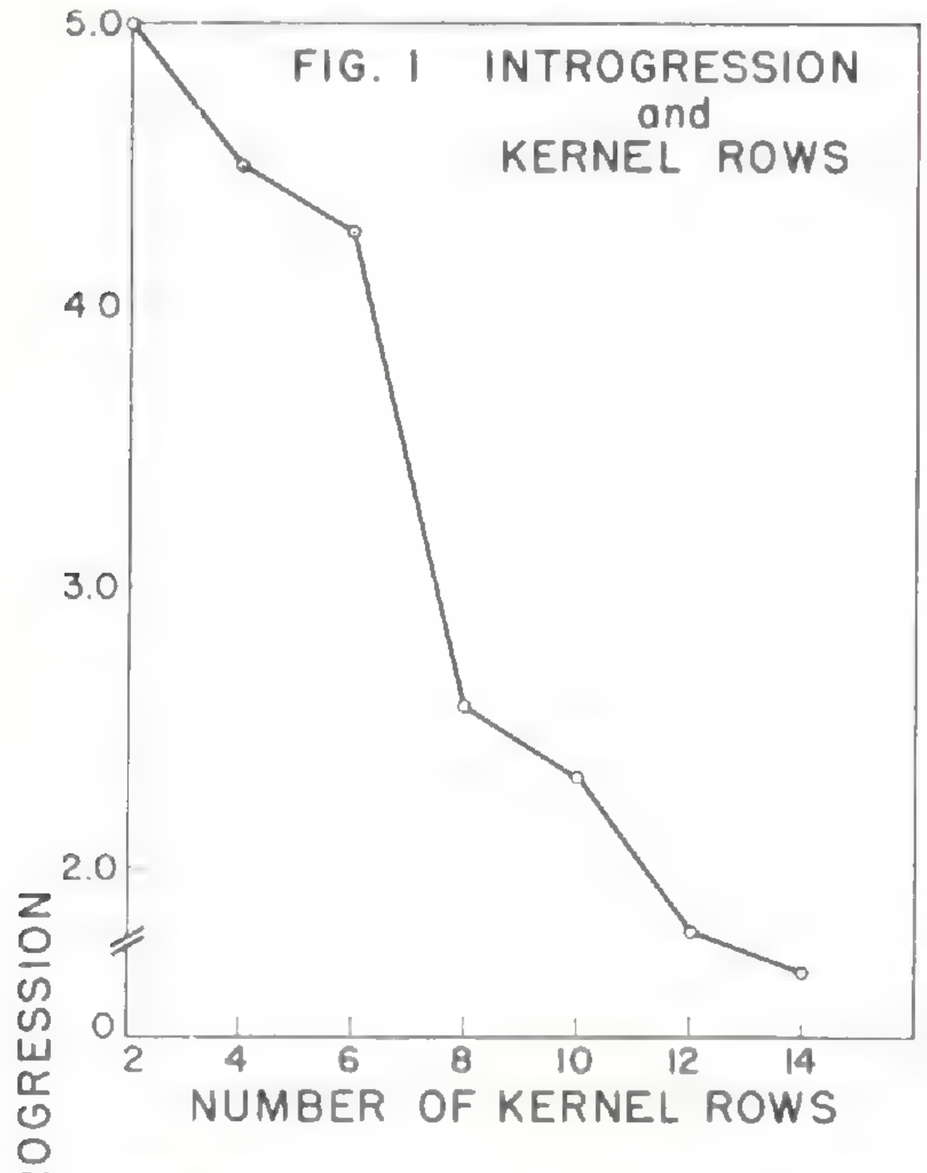


FIG. 1 INTROGRESSION and KERNEL ROWS
5.0
4.0
3.0
2.0
0
2
4
6
8
10
12
14
NUMBER OF KERNEL ROWS
AVERAGE ESTIMATE OF TEOSINITE INTROGRESSION

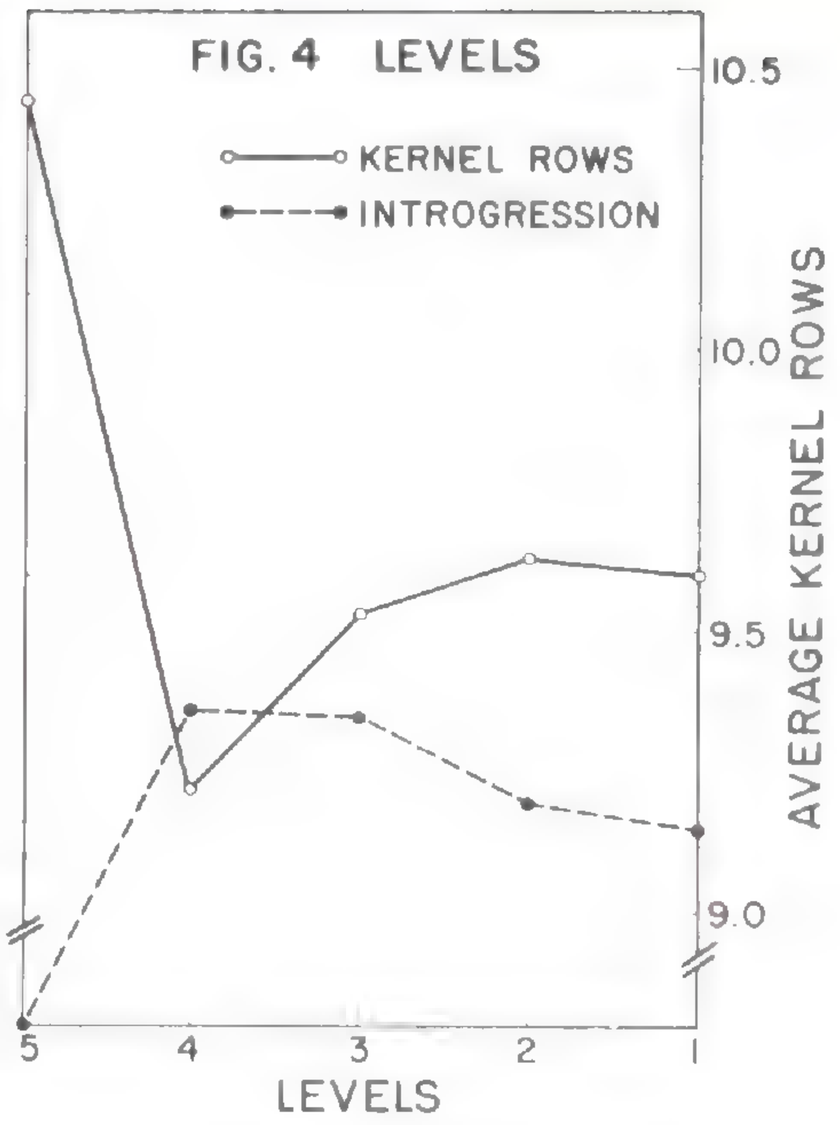


FIG. 4 LEVELS
KERNEL ROWS
INTROGRESSION
10.5
10.0
9.5
9.0
5
4
3
2
1
LEVELS
AVERAGE KERNEL ROWS

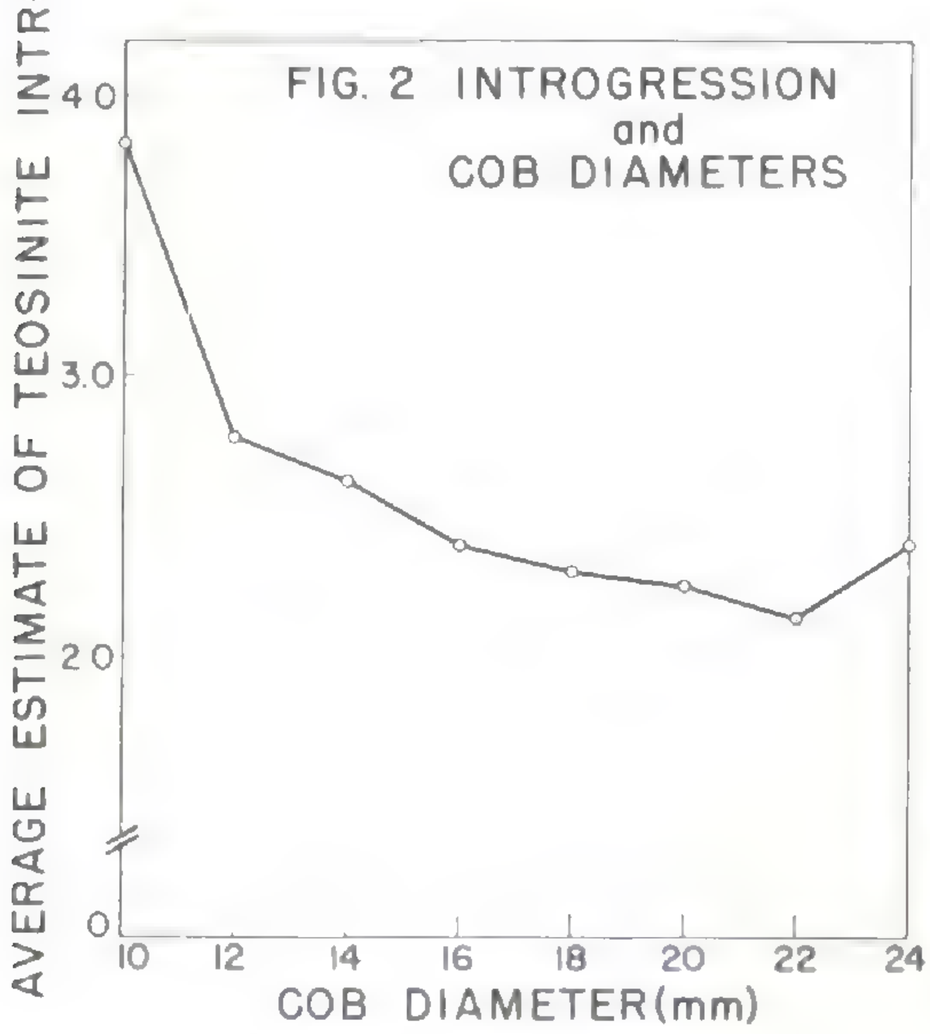


FIG. 2 INTROGRESSION and COB DIAMETERS
4.0
3.0
2.0
0
10
12
14
16
18
20
22
24
COB DIAMETER(mm)
AVERAGE ESTIMATE OF TEOSINITE INTROGRESSION

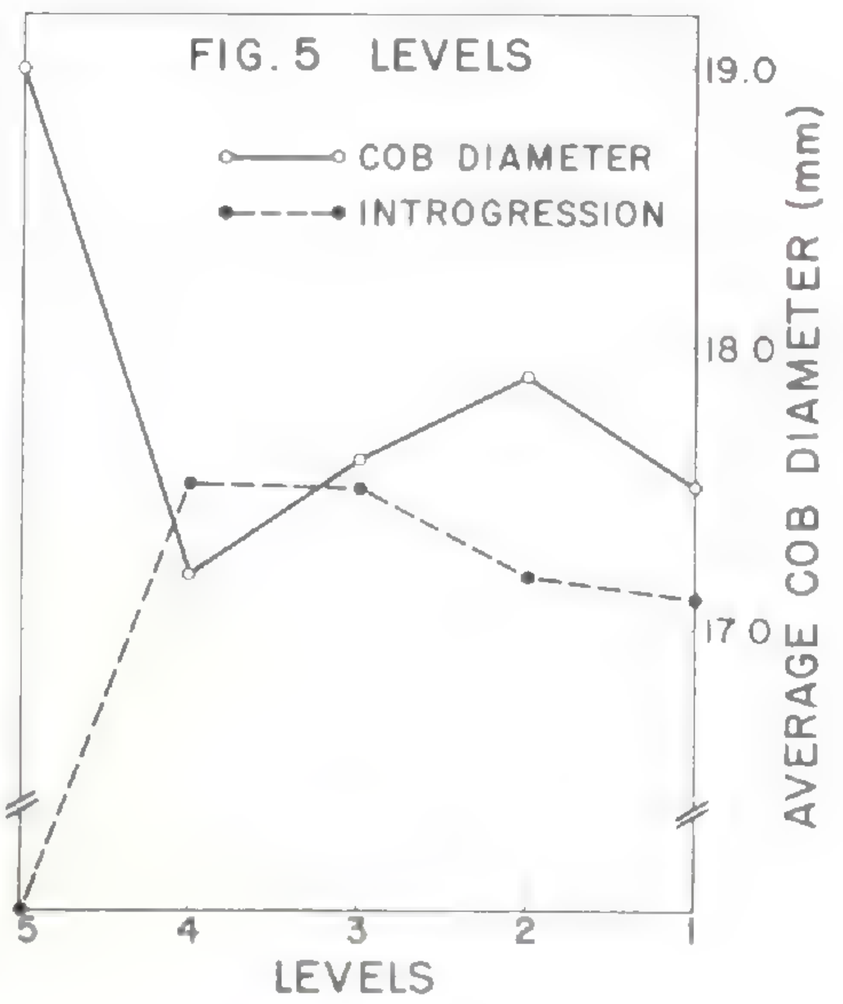


FIG. 5 LEVELS
COB DIAMETER
INTROGRESSION
19.0
18.0
17.0
5
4
3
2
1
LEVELS
AVERAGE COB DIAMETER (mm)

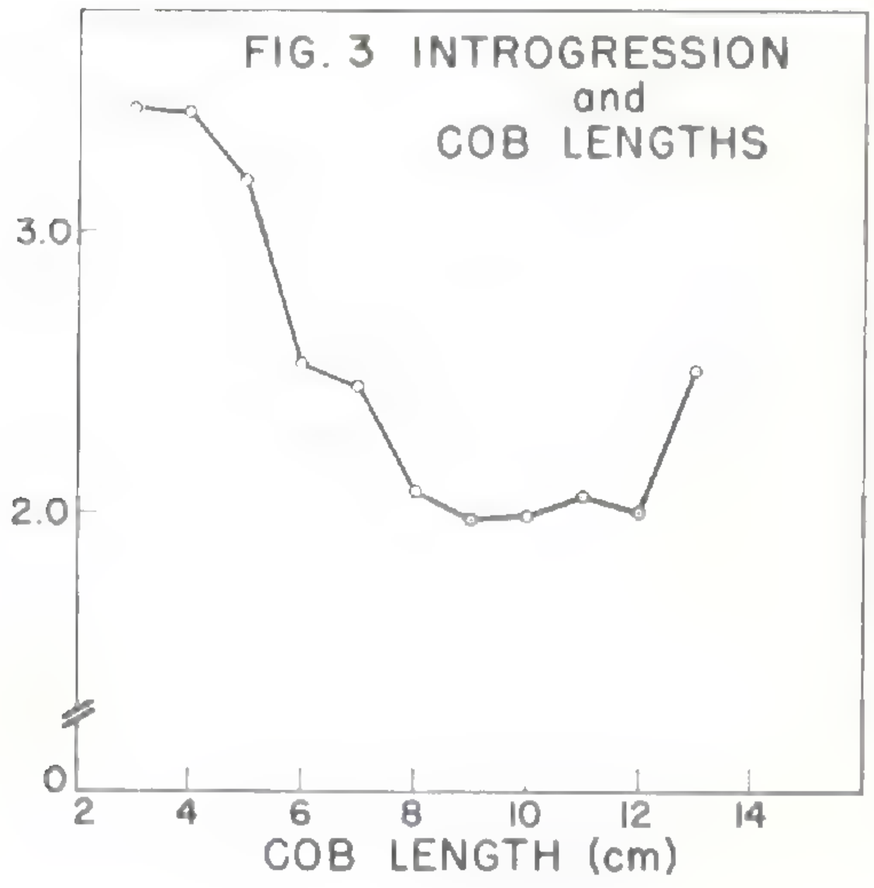


FIG. 3 INTROGRESSION and COB LENGTHS
3.0
2.0
0
2
4
6
8
10
12
14
COB LENGTH (cm)

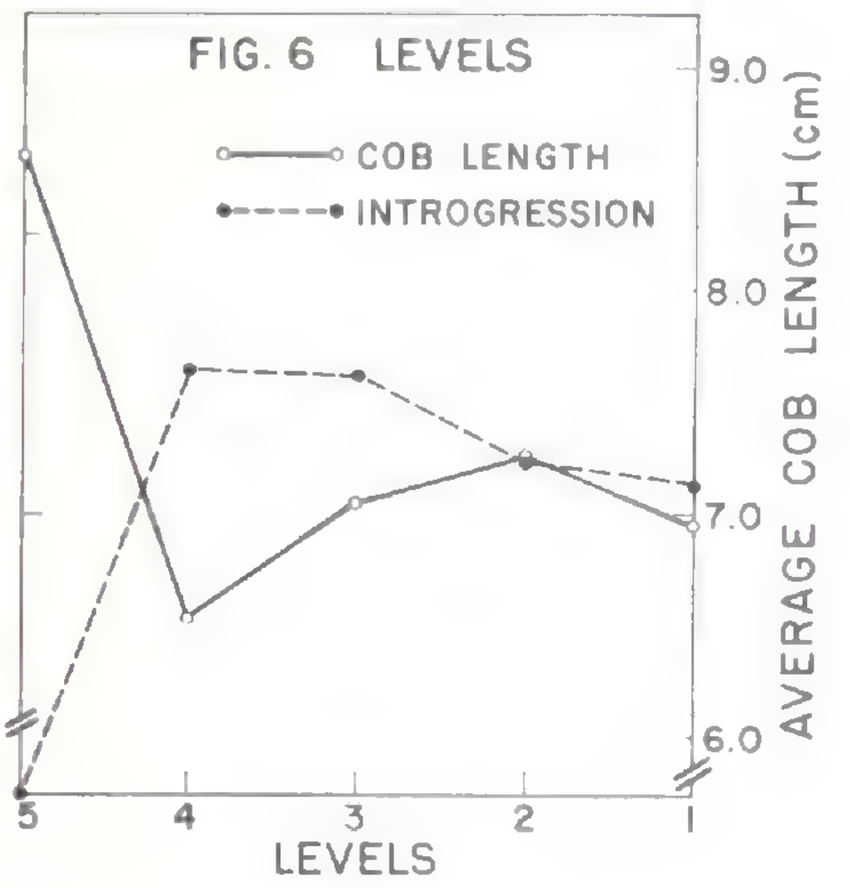


FIG. 6 LEVELS
COB LENGTH
INTROGRESSION
9.0
8.0
7.0
6.0
5
4
3
2
1
LEVELS
AVERAGE COB LENGTH (cm)

from grain production and into the production of strong lignification of the cob and stalk tissues. But even so, such an expenditure on development of a stiff stalk may be necessary to keep the ears erect and away from certain vermin.

The effect of teosinte introgression on cob length is not always detrimental. The longest, as well as the shortest, intact cobs were the most Tripsacoid (fig. 3). Those of intermediate length tended to resemble the original maize in having soft glumes.

The same type of parabolic curvilinear correlation between teosinte introgression and cob-length was also found with the cobs from Richards Cave in Arizona (Galinat *et al.*, 1956). In this previous study the parabolic curvilinear correlation, based on 433 intact cobs, had a value of 0.859, which was highly significant. The nature of the curve was explained by assuming that the long Tripsacoid cobs are the vigorous products of heterozygous teosinte germplasm, while their short counterparts are the detrimental effects of homozygous teosinte germplasm. This explanation may be applied equally well to the cobs from Cebollita Cave. The repetition of the so-called "maize-teosinte heterosis" at another site, indicates that this apparent counterpart of modern hybrid maize may have become widespread at the time just prior to 1200 A.D. in the Southwest. The blending of teosinte germplasm into maize would continue if its presence provided any selective advantage such as that resulting from maize-teosinte heterosis. Under such conditions, the distribution of Tripsacoid maize might become many generations and hundreds of miles removed from teosinte itself.

Level 3 Maize

Level 3 marks the start of a progressive reduction in teosinte contamination or at least a modification of its

expression. In either case, as the indurative effects of this introgression[1] declined, the average cob size retrogressed somewhat toward that of the original pure Chapalote. The reduction in "introgression" was slow at first, being only 8% at this stratum (Level 3) and not in proportion to the far greater recovery in kernel row number, cob diameter, and cob length of 18%, 22%, and 21% respectively (Plate XXIV, figs. 4, 5, 6).

But even as the direct effects of teosinte introgression were apparently diminishing, the variability in cob size which was introduced by this introgression in the previous Level (4), continued to increase in higher levels. For cob diameter, the standard deviations which measure degree of variability, for Levels 5 through 1, were 1.48 mm., 2.12 mm., 2.56 mm., 2.54 mm., and 2.10 mm., respectively. Increases in diameter variance are significant up to Level 3. But for cob length, the expanding variation proceeds one level higher, as shown by the standard deviations for Levels 5 to 1, respectively, as follows: 1.01 cm., 1.89 cm., 2.27 cm., 2.39 cm., and 1.86 cm.

There are several possibilities which may, as a whole or in part, account for the continued increase in variability after a reduction in teosinte introgression. If there was some variability injected by a new non-Tripsacoid race from elsewhere, its effect must have been insignificant because the continuity of the population was not disrupted by a complete break from the features of Chapalote. In addition to an actual reduction in teosinte germplasm, the accumulating variability may have brought about some modification of its indurative effects. Mangelsdorf (1958) suggested, on the basis of experimental

[1] In order to facilitate further discussion, we shall assume that our estimate of teosinte introgression, according to the degree of induration, represents a relative measure of its intensity.

evidence from modern maize-teosinte derivatives, that much of the variation in modern maize is the product not only of recombination of genes from the two species, but also from the mutagenic effects of teosinte germplasm in maize. Similarly, some of the increased variation in the Cebollita maize may be the result of a mutagenic effect of teosinte germplasm.

Level 2 Maize

Proceeding to the next Level (2), the same trends continue: teosinte introgression decreases while average ear-size increases. The extremes in cob-length and cob-diameter held about the same as those of the previous level (Table II). But in the case of cob-length, the various categories became more equally represented with the result that the standard deviation or variability increased. As mentioned previously, the longest cobs are apparently a product of maize-teosinte heterosis. The fact that cob length did not decline with the apparent reduction in introgression at these higher levels might be explained in terms of a selective elimination of deleterious factors from teosinte and/or a buffering against the effects of such factors while beneficial factors involved in maize-teosinte heterosis were retained and blended into the evolving population.

Level 1 Maize

The cobs from the uppermost level represent the final evolutionary product from this site. Although the actual quantity of cobs was less than ten per cent of that from any previous level, it yields some of the longest and best specimens. These superior ears represent a combination of butt fasciation descended from the original Chapalote together with the more lignified and heterotic products of teosinte introgression. Some of these specimens re-

semble the present day maize from the Southwest (Plate XXIII, cob I).

Summary

1. The method of scoring for teosinte introgression according to the degree of induration has been used to study the archaeological record of the role of such introgression in the evolution of 2575 cobs found in five successive strata in Cebollita Cave in New Mexico.

2. The evolutionary sequence starts at Level 5 with a pure type of Chapalote, the indigenous race from this part of North America. Identification of this original Cebollita maize as Chapalote was possible because its morphological details were perfectly preserved by carbonization.

3. After a period of abandonment of the cave most of the maize in Level 4 changed abruptly to a highly Tripsacoid type of Chapalote which was becoming prevalent in the Southwest. Some of the more Tripsacoid of these specimens resembled, in induration and appearance, segregates from experimental hybrids between maize and teosinte, while other specimens remained identical to the original pure type.

4. The immediate effect of the teosinte introgression was to cause a marked reduction in average cob-size to the lowest values of the site.

5. Although advances to higher Levels (3, 2, 1) were marked by a progressive decrease in the indurative effects of this introgression, the variability in cob size which was introduced by the introgression continued to increase. For cob diameter, increases in variation cease at Level

3. But for cob length, the expanding variation proceeds up one level higher.

6. The same type of parabolic relationship between teosinte introgression and cob-length which was found in a previous study of cobs from Richards Cave in Arizona was also found in the Cebollita Cave cobs. The interpretation of this type of relationship is that the long Tripsacoid cobs are the vigorous products of heterozygous teosinte germplasm, while their short counterparts show the detrimental effects of homozygous teosinte germplasm.

7. In the final evolutionary products from Levels 2 and 1 at Cebollita, there is almost complete recovery from the detrimental effects of teosinte introgression and many of the cobs are larger and probably more productive than the original Chapalote maize. Some of these superior cobs resemble those of the present day maize from the Southwest.

Acknowledgment

During the course of the investigation and preparation of the manuscript, many helpful suggestions were made by Professor Paul C. Mangelsdorf of Harvard University.

TABLE I. A comparison of the ear characteristics of archaeological maize from Cebollita and Cottonwood Caves to that of modern Chapalote from Mexico.

	Cebollita	Cottonwood[1]	Chapalote[2]
External Characters of Ear			
Length (cm.)	8.7	9.0	11.0
Diameter (cm.)	2.6	3.3	2.9
Row Number	10.5	14.0	12.3
Width of Kernel (mm.)	6.0	6.0	6.7
Thickness of Kernel (mm.)	4.0	4.0	4.1
Length of Kernel (mm.)	7.1	—	7.4
Internal Characters of Ear			
Diameter of Cob (mm.)	19.0	—	22.0
Diameter of Rachis (mm.)	12.0	—	11.2
Length of Rachilla (mm.)	2.0	—	1.8
Glumes	prominent	prominent	prominent
Cupule Wings	prominent	—	prominent
Teosinte Introgression	1	—	—

[1] Data from Hurst and Anderson (1949).
[2] Data from Wellhausen *et al.* (1952).

TABLE II. Morphological characteristics of five strata of archaeological maize cobs.

		Level 5	Level 4	Level 3	Level 2	Level 1
Total population		200	613	798	903	61
Carbonized %		85	44	0	0	0
Charred %		15	1	0	0	0
Intact %		7	10	27	23	33
Fasciated %		27	18	20	21	23
Unusual %		3	5	3	4	4
Teosinte Introgression (%)	1 (low)	100	15	18	20	25
	2	—	37	38	48	50
	3	—	30	22	24	12
	4	—	15	19	7	5
	5 (high)	—	3	3	1	1
No. of Kernel Rows (%)	4	—	3	2	1	2
	6	—	—	1	1	—
	8	27	48	39	39	38
	10	32	30	35	35	41
	12	33	16	20	21	16
	14	5	2	2	3	3
	16	3	—	—	—	—
Diameter mm. (%)	10	—	—	1	—	—
	12	—	3	4	2	—
	14	—	14	11	11	11
	16	10	24	24	20	35
	18	40	39	31	30	32
	20	48	18	23	29	16
	22	5	2	5	6	6
	24	—	—	1	1	—
	26	—	—	—	1	—
Length cm. (%)	3	—	—	3	2	—
	4	—	8	7	10	5
	5	—	29	15	17	15
	6	—	19	22	17	20
	7	11	20	17	14	20
	8	34	9	13	14	15
	9	25	7	8	9	10
	10	30	4	6	8	10
	11	—	—	4	5	—
	12	—	4	3	4	—
	13	—	—	1	—	—
	14	—	—	1	—	5
	15	—	—	—	1	—

— Absent

LITERATURE CITED

Bluhm, Elaine, 1952. Clothing and textiles, Part VI, Mogollon culture continuity and change. Fieldiana: Anthropology 40, Chicago Nat. Hist. Mus.

Cosgrove, C. B., 1947. Caves of the upper Gila and Hueco areas in New Mexico and Texas. Papers of the Peabody Museum, Harvard Univ. 24: 1–181.

Galinat, W. C., P. C. Mangelsdorf and L. Pierson, 1956. Estimates of Teosinte introgression in archaeological maize. Bot. Mus. Leafl. Harvard Univ. 17: 101–124.

Grobman, A. and P. C. Mangelsdorf, 1959. Evidence for existence of a common prehistoric race in both North and South America. Maize Gen. Coop. News Letter 33: 28.

Haury, Emil, 1934. The Canyon Creek ruin and the cliff dwellings of the Sierra Ancha. Medallion Papers 14, Gila Pueblo-Globe, Arizona.

Hurst, C. T. and E. Anderson, 1949. A corn cache from western Colorado. Amer. Antiquity 14: 161–167.

Kidder, A. V. and S. J. Guernsey, 1919. Archaeological explorations in northeastern Arizona. Bur. Amer. Ethnology Bulletin 65. Washington.

Mangelsdorf, P. C., 1954. New evidence on the origin and ancestry of maize. Amer. Antiquity 19: 409–410.

——, 1958. The mutagenic effect of hybridizing maize and teosinte. Cold Spring Harbor Symp. Quant. Biol. 23: 409–421.

—— and C. E. Smith, Jr., 1949. New archaeological evidence on evolution in maize. Bot. Mus. Leafl. Harvard Univ. 13: 213–247.

—— and R. H. Lister, 1956. Archaeological evidence on the evolution of maize in northwestern Mexico. Bot. Mus. Leafl. Harvard Univ. 17: 151–178.

Reeves, R. G. and P. C. Mangelsdorf, 1942. A proposed taxonomic change in the tribe Maydeae (family Gramineae). Amer. Jour. Bot. 29: 815–817.

Wellhausen, E. J., L. M. Roberts and E. Hernandez X. *in collaboration with* P. C. Mangelsdorf, 1952. Races of maize in Mexico. Bussey Institution of Harvard University.

BOTANICAL MUSEUM LEAFLETS
HARVARD UNIVERSITY

CAMBRIDGE, MASSACHUSETTS, JUNE 30, 1961 VOL. 19, NO. 9

CARLUDOVICA PALMATA IN BROOMMAKING

BY

MELVIN LEE BRISTOL

Carludovica palmata Ruíz & Pavon is best known as the source material for "Panama" hats, the majority of which are manufactured in Ecuador (2).[1] The leaves are also used to a lesser extent for matting, curtains, roofing, baskets, cigar-cases, purses, fly swatters and brooms (2, 3, 4). The petioles, when divided into strips, are used for making brooms in Honduras (1).

At the eastern base of the Cordillera Oriental in the Comisaría del Putumayo in southern Colombia, I recently encountered a household industry of broommaking from the dried leaf blades of *Carludovica palmata*, known locally as *iraca*. The brooms are made sporadically throughout the year at the convenience of the women of the household and are sold to an agent in the nearby town of Mocoa for twenty to twenty-five centavos each. Sent to the markets in the highland city of Pasto, they are resold for fifty to sixty centavos.

The procedure of broommaking begins with the collection of young, partially expanded leaf blades from plants in the vicinity of the house. They are spread on the ground near the home to dry in the sun for about four days, after which they are hung over a line strung be-

[1] See References.

tween posts of the porch roof. Here they remain indefinitely until the housewife makes or obtains a light cord of *cabuya* (*Agave* spp.). When she is ready to begin to make a broom, the remaining two to four centimeters of petiole are cut from the leaves with a machete, but the leaf veins (or fibres) are carefully left coherent at their

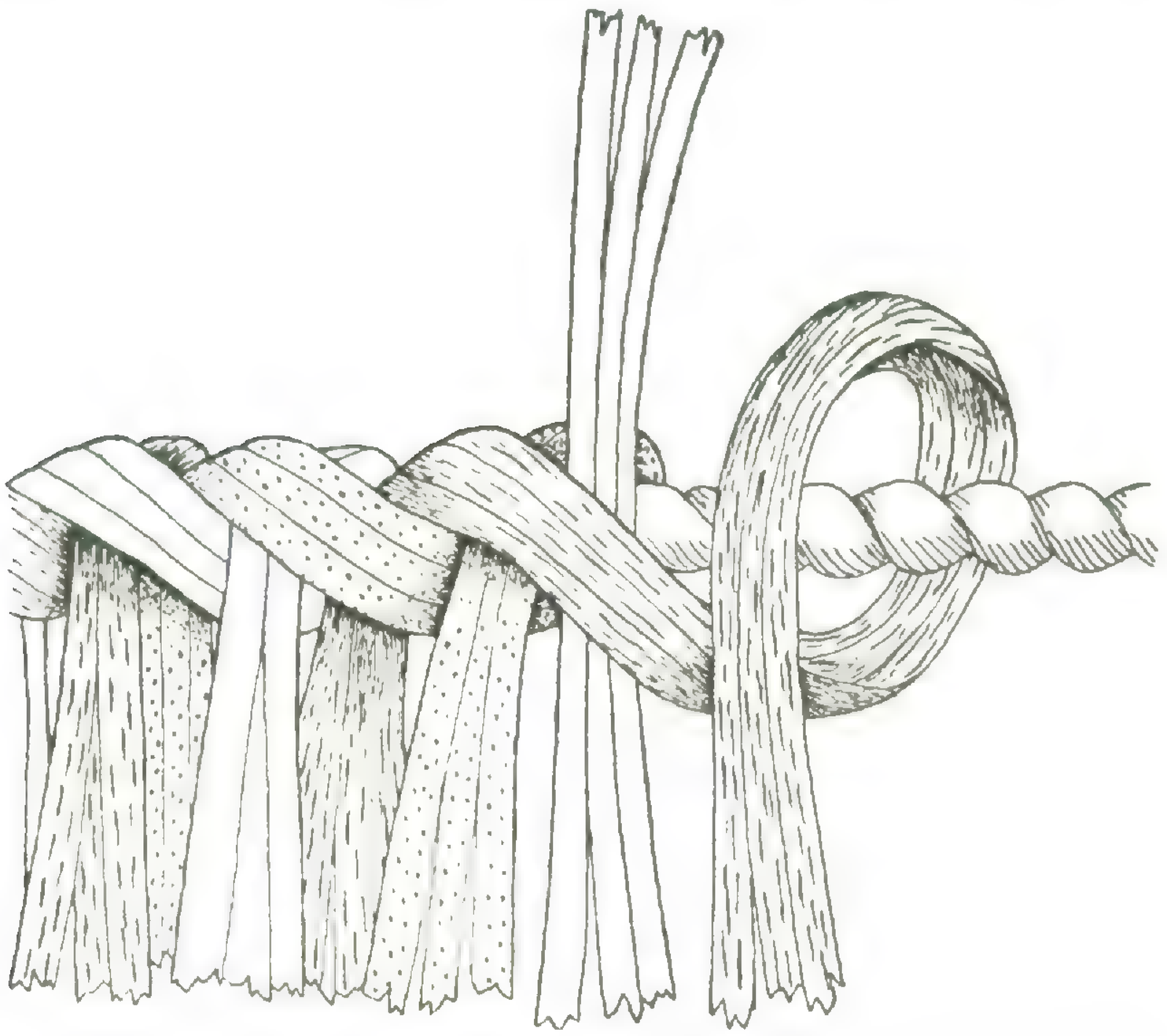


FIGURE 1. Method of tying bundles of fibres to the cord. The center of each bundle is placed against the near side of the cord and the upper half of the previous bundle is brought down in front, looped around the cord and pulled snug.

bases and are then pulled apart by hand. Why this is not done in one action with the machete is not apparent, for separating the fibres by hand takes several seemingly unnecessary minutes. Perhaps conserving the tough bases of the fibres affords the product a longer life.

The cord is now stretched tautly across a corner of the porch at a height of about three feet. While working in a sitting position, the woman finds this a convenient height for making the broom. Beginning near one end,

she ties small bundles of the fibres at their centres to the cord so that both ends hang down (text fig. 1). Each knot may be tied with from three to about fifteen fibres, but the number is relatively constant for each broom. When many fibres are used, the knots are large, giving the completed product a knobby aspect at the top. It is unlikely that the life of the broom is different with either method, since both types of broom contain an equal number of fibres; possibly the size of bundle used for knotting caters to various aesthetic values of the consumers. Certainly knotting with large bundles is a more rapid method. Because some brooms are knotted with small bundles of fibres, it may be that aesthetic considerations are of more importance in this area than is economy of time.

The fibres are tied closely along the cord for a distance of about one and a half meters, and when finished look like a grass skirt about twenty-five centimeters long. Untied from the porch railing, this "skirt" is rolled spirally on the end of a stick and securely bound. A few fibres which are too long are then trimmed off the end with a machete.

When the broom is made for home consumption it is immediately provided with a handle. When it is to be sent to urban centers, however, it is rolled into a bundle without a handle, for the consumer simply unrolls a worn out "skirt" from his old broomstick and replaces it with the new one.

REFERENCES

1. Corrêa, M. P. 1926. Dicionário das Plantas Uteis do Brasil e das Exóticas Cultivadas. Vol. I, p. 319. Rio de Janeiro.

2. Harling, G. 1958. Monograph of the Cyclanthaceae. Acta Horti Bergiani 18: 1–428 (p. 117). Lund.

3. Pérez-Arbeláez, E. 1956. Plantas Utiles de Colombia. Bogotá. p. 278.

4. Portillo, A. 1951. Divulgación de Conocimientos Científicos sobre las Plantas más Utiles y Conocidas en Colombia, su Valor Alimenticio, Medicinal e Industrial. pp. 462–464. Pasto.

EXPLANATION OF THE ILLUSTRATION

PLATE XXV. (*Upper*) *Carludovica palmata* Ruíz & Pav. near Mocoa, Comisaría del Putumayo, Colombia.

(*Lower*) Housewife with dried leaf blades of *C. palmata* on porch.

Photographs by M. L. BRISTOL

Plate XXV

EXPLANATION OF THE ILLUSTRATION

PLATE XXVI. (*Upper*) Tying bundles of 3–5 fibres to the cord, as in Fig. 1.

(*Lower left*) A new broom before trimming (left), and an old worn one (right).

(*Lower right*) Top of broom securely bound to handle. Bundles of 8–10 fibres were tied to the cord in this example.

Photographs by M. L. BRISTOL

Plate XXVI

NEONELSONIA—A COLOMBIAN FOLK MEDICINE

BY
MELVIN LEE BRISTOL

IN August 1960, I studied the varieties of *arracacha*, the umbelliferous *Arracacia xanthorhiza* Bancroft, in the Colombian Andes. On one occasion during the study, in the Indian village of Sibundoy (near Pasto) in the Comisaría del Putumayo, a small boy led me to a growth of what he termed "wild arracachas." It was a coarse tangle of an umbelliferous plant clambering over shrubs in an area of 15 square meters. Since this "wild arracacha" appeared to me to be very closely related to the genus I was studying, if not the same, I collected specimens in flower and fruit. When I took them back to one of the older Sibundoy Indians, Juan Pedro Chindoy, he called the plant "íngo-sha-hush" in the Kamsá language.

Utilization

The man told me that the plant is used as a remedy for swelling and inflammation of the upper region of the intestine (*hinchazones intestinales superiores*). Furthermore, he said that it is employed by all Sibundoy women immediately after childbirth "to prevent their death." In both cases, the preparation and dosage is the same: the leaves and stems are boiled well, then some sugar and ten drops of a distilled alcoholic beverage (*trago*) are

added. One-half demitasse cupful (15 cc.?) is taken internally.

Taxonomy

I have identified the Sibundoy "íngo-sha-hush" as *Neonelsonia acuminata* (Bentham) Coulter & Rose ex Drude. *Neonelsonia*, described in 1895 by Coulter and Rose (4), comprises two species: the type, *Neonelsonia ovata* of the mountains of southern Mexico; and the species under consideration here. *Neonelsonia acuminata* is a scandent, herbaceous, essentially glabrous perennial with a long, woody taproot. The leaves are ternately compound with ovate to lanceolate, spinulose-serrate leaflets often lobed toward the base. The compound umbels lack an involucre but possess filiform involucels which frequently surpass the fertile pedicels in length. The greenish yellow petals are obcordate, with a narrow, inflexed tip. The ellipsoid-cordate fruits have five prominent, fleshy ridges.

Neonelsonia acuminata bears many resemblances to various species of *Arracacia*, particularly, as noted by Constance (3), to *A. Pennellii* Constance, *A. Wigginsii* Constance and *A. elata* Wolff. Mathias and Constance (6) recognized six differences between *Neonelsonia* and *Arracacia*. Four of these differences—the shape of the petal apex, the degree of reduction of the calyx, the position of the oil ducts, and the shape of the groove on the seed face—seem unimportant, for upon examination these characters are seen to grade from one genus to the other. Of greater importance in distinguishing these two genera is the wrinkled surface of the fruits of *Neonelsonia*, possibly lacking schlerenchymatous tissue, and more especially, their ellipsoid-cordate form.

Examination of sixteen type specimens of *Arracacia* in the Harvard University Herbarium shows that the

fruit varies from lanceolate and oblong to ovate, but that none are ellipsoid-cordate. In view of the many resemblances between these two genera, however, it is possible that a future monographer of *Arracacia* might emend the genus-concept to include *Neonelsonia*.

Distribution

Specimens of *Neonelsonia acuminata* in the Harvard University Herbarium indicate that its range is Colombian and Ecuadorean, extending from the Departamento del Cauca in the north to the Provincia de Azuay in the south at elevations of 2450 to 3660 meters. My specimens from Sibundoy in the Comisaría del Putumayo, Colombia, were collected at 2100 meters, extending the known altitudinal limits of the species. Another collection, from San Diego near Guachucal, Nariño, is within the previously known range.

Because *Neonelsonia acuminata* is not readily distinguished in the field from *Arracacia Pennellii* and from *A. Wigginsii* when fruits are not available, it is well to note the distribution of these two species of *Arracacia* in central Colombia and central Ecuador, overlapping the range of *N. acuminata*. The specimens of *Arracacia Pennellii* available to Constance (3) when the species was described came from Cundinamarca, Norte de Santander and Santander in Colombia at elevations of 3000 to 3800 meters. Likewise, the specimens of *Arracacia Wigginsii* were collected in Cañar and Azuay (one at 3660 meters) in Ecuador. A later collection, now in the Harvard University Herbarium, is also from Azuay but at 2740 meters. Our present scanty knowledge indicates that of these three species, only *Neonelsonia acuminata* is found in southern Colombia and northern Ecuador and that its altitudinal tolerance extends to lower elevations than does that of the two species of *Arracacia*.

Specimens of *Nconelsonia acuminata* examined

Colombia. Cauca: 3100–3300 m. alt., June 11–13, 1922, *Pennell & Killip 6632, 6676.* Putumayo: 2100 m. alt., August 3, 1960, *Bristol 240.* Nariño: 3140 m. alt., August 10, 1960, *Bristol 241.* Ecuador. Pichincha: 3000–3600 m. alt., August 13, 1923, *Hitchcock 20881;* March 31, 1920, *Holmgren 449;* 12,000–12,600 ft. alt., 1855, *Couthouy.* Azuay: 8000–9000 ft. alt., July 27–August 12, 1945, *Camp E 4503.*

REFERENCES

1. Bancroft. 1825. Trans. Agric. Hort. Soc. Jamaica 1825, 3.

2. Bentham, G. 1845. Plantae Hartwegianae. London. 187.

3. Constance, L. 1949. The South American species of *Arracacia* (Umbelliferae) and some related genera. Bull. Torr. Bot. Club 76: 39–52.

4. Coulter, J. M. & J. N. Rose. 1895. Contr. U.S. Nat. Herb. 3: 306.

5. Drude, O. 1898. Umbelliferae *in* Natürlichen Pflanzenfamilien 3 (8): 167. Leipzig.

6. Mathias, M. E. & L. Constance. 1944. Umbelliferae (Pars) *in* North American Flora 28B, 43–160. New York.

NOVELTIES IN THE ORCHID FLORA OF THE GUAYANA HIGHLANDS*

BY
CHARLES SCHWEINFURTH

THE present paper, which is the first of two articles dealing with novelties in the Orchidaceae of the Guayana Highlands, treats eleven new species. The order follows that of the System proposed by Dr. Rudolph Schlechter in Notizblatt des Botanischen Gartens und Museums, Berlin-Dahlem 9, No. 88 (1926) 563–591.

Duckeella alticola *C. Schweinfurth sp. nov.*

Herba terrestris, pro genere robusta, nigrescens, circiter 50 cm. alta. Caulis glaber, saepissime superne inaequaliter bifurcatus. Folia valde coriacea, biformia; basalia pauca, oblongo-linearia, acuta, suberecta, usque ad 19 vel 22 cm. longa et 9–16 mm. lata; caulina duo, multo breviora, remotissima, elliptico-oblonga, acuta, 8.7–10 cm. longa, usque ad 1.3 cm. lata. Racemi in ramorum apice, densius pauci- vel pluriflori. Flores mediocres, aurei. Sepala crassa, concava, marginibus incurvis. Sepalum dorsale oblongo-ellipticum, acutum, circiter 2 cm. longum et 8.2 mm. latum. Sepala lateralia persimilia, dorso carinata. Petala latiora, ovalia vel late

* For the privilege of studying the extensive collections recently made in this region, I am indebted chiefly to a grant from the National Science Foundation.

EXPLANATION OF THE ILLUSTRATION

PLATE XXVII. DUCKEELLA ALTICOLA *C. Schweinfurth.* 1, plant, one third natural size. 2, flower expanded, one and one quarter times natural size. 3, column and lip, three quarters view, two and one quarter times natural size.

Drawn by ELMER W. SMITH

Plate XXVII

elliptica, submembranacea, circiter 1.8 cm. longa et 1.2 cm. lata. Labellum in circuitu oblongum, circiter 1.75 cm. longum et 8 mm. latum, basi trilobatum cum lobulis parvis semiorbicularibus, apice truncato abrupte acutum; discus inter lobos laterales callo brevi pluristriato emarginato ornatus. Columna comparate parva, circiter 8 mm. alta, cucullata, apice bifida, basi dente oblongo prominenti utrinque praedita.

This orchid differs conspicuously from the other species of Duckeella in having broader leaves, fleshy, concave and acute sepals, a relatively short callus on the lip and a pair of conspicuous teeth on the column. It is a comparatively robust plant of consistently rather high altitudes.

AMAZONAS: Cerro Duida, moist slopes of Savanna Hills, 1350 meters altitude, August 1928–April 1929, *G. H. H. Tate 736;* Cerro Sipapo (Paráque), near summit of West Peak, at 1750 meters altitude, infrequent in bogs, flowers yellow, fragrant, December 20, 1948, *Bassett Maguire & Louis Politi 27797.* BOLÍVAR: Cerro Guaiquinima, Río Paragua, occasional near Cumbre Camp, at 2000 meters altitude, flowers dull yellow, December 25, 1951, *B. Maguire 32748;* Same locality, rare in bog, along west escarpment rim 1 km. west of Cumbre Camp, at 1800 meters altitude, flowers yellow, December 30, 1951, *B. Maguire 32830, 32839A;* Same locality, frequent in bogs, "North Valley," at 1600–1700 meters altitude, flowers yellow with the outer members [sepals] bronze outside, January 4, 1952, *B. Maguire 32973* (TYPE in Herb. Ames No. 69538).

Sobralia speciosa *C. Schweinfurth sp. nov.*

Herba elata, speciosa, terrestris, 1–3 metralis (fide collectoris). Caules plusminusve robusti, vaginis longe tubularibus arctis glabris obtecti. Folia numerosa, disticha, lanceolata vel ovato-lanceolata, longe acuminata, plicata, supra nitentia, usque ad 15 cm. longa et 3.7 cm. lata. Inflorescentiae saepissime laterales (raro terminales), racemosae, laxe pauciflorae, suberectae. Flores magni spectabilesque, purpurei, membranacei. Sepalum dorsale oblongo-oblanceolatum, acutum, circiter 4.5–5.5 cm. longum et 1.3 cm. latum. Sepala lateralia similia, an-

guste oblanceolato-oblonga, paulo obliqua, dorso carinata, circiter 5–5.6 cm. longa et 1.3 cm. lata. Petala oblongo-obovata, apice late rotundata, sepalis latiora, circiter 2–3 cm. lata. Labellum majus, segmenta cetera superans, in positu naturali convolutum, expansum suborbiculari-ellipticum, circiter 6–7 cm. longum et 5 cm. latum, apice profunde bilobatum; discus carinis pluribus superne laceris percursus. Columna circiter 3–3.5 cm. alta, apice falcula incurva utrinque ornata.

This species appears to be related to the Peruvian *Sobralia Weberbaueriana* Kränzl., but has smooth (not furfuraceous) sheaths, much smaller leaves and a dissimilar lip and column.

AMAZONAS: Cerro de la Neblina, Río Yatua, near Cumbre Camp, at 1700 meters altitude, occasional on low bushy slopes, "roots fleshy; corolla cerise; lip with median yellow line and several white lines; column whitish, pink-flushed," January 4, 1954, *Bassett Maguire, John J. Wurdack & George S. Bunting 37028;* Same locality, occasional in scrub forest 1 kilometer north of Cumbre Camp, at 1800 meters altitude, "fls. rich pink," January 10, 1954, *Maguire, Wurdack & Bunting 37202;* Same locality, locally frequent in scrub forest near Cumbre Camp, at 1800 meters altitude, "fls. magenta, the lip with subapical white area," November 19, 1957, *Bassett Maguire, John J. Wurdack & Celia K. Maguire 42142* (TYPE in Herb. Ames No. 69507).

Stelis latisepala *C. Schweinfurth sp. nov.*

Herba pusilla, caespitosa, epiphytica, 4–5 cm. alta. Caulis abbreviatus, circiter 3 mm. altus, vaginis laxis tubularibus omnino celatus. Folium erectum, oblanceolatum vel obovato-spathulatum, apice rotundatum, sessile, 8–14 mm. longum, expansum usque ad 4.2 mm. latum. Inflorescentia singula, folium multo superans, supra laxe pluriflora, usque ad 4.7 cm. longa. Flores perparvi, subcarnosi. Sepala transverse rhombico-ovata, acuta, trinervia, basi connata. Sepalum dorsale circiter 2.6 mm. longum et 3 mm. latum. Sepala lateralia similia sed minora, valde obliqua, usque ad 2 mm. longa et 2.5

EXPLANATION OF THE ILLUSTRATION

PLATE XXVIII. SOBRALIA SPECIOSA *C. Schweinfurth.* 1, plant, about one half natural size. 2, dorsal sepal, three quarters natural size. 3, petal, three quarters natural size. 4, lateral sepal, three quarters natural size. 5, lip, three quarters natural size. 6, column from side, three quarters natural size.

Drawn by ELMER W. SMITH

Plate XXVIII

mm. lata. Petala minuta, rhombico-ovata, supra multo incrassata, circiter 0.7 mm. longa et 0.9 mm. lata. Labellum simplex, petalis simile, rhombico-ovatum, circiter 0.6 mm. longum et 0.9 mm. latum; discus callo carnoso transverso bilobato prope medium ornatus. Columna generis, minuta, supra abrupte dilatata.

This little plant seems to be allied to the Brazilian *Stelis parvifolia* Garay, but has larger glabrous flowers.

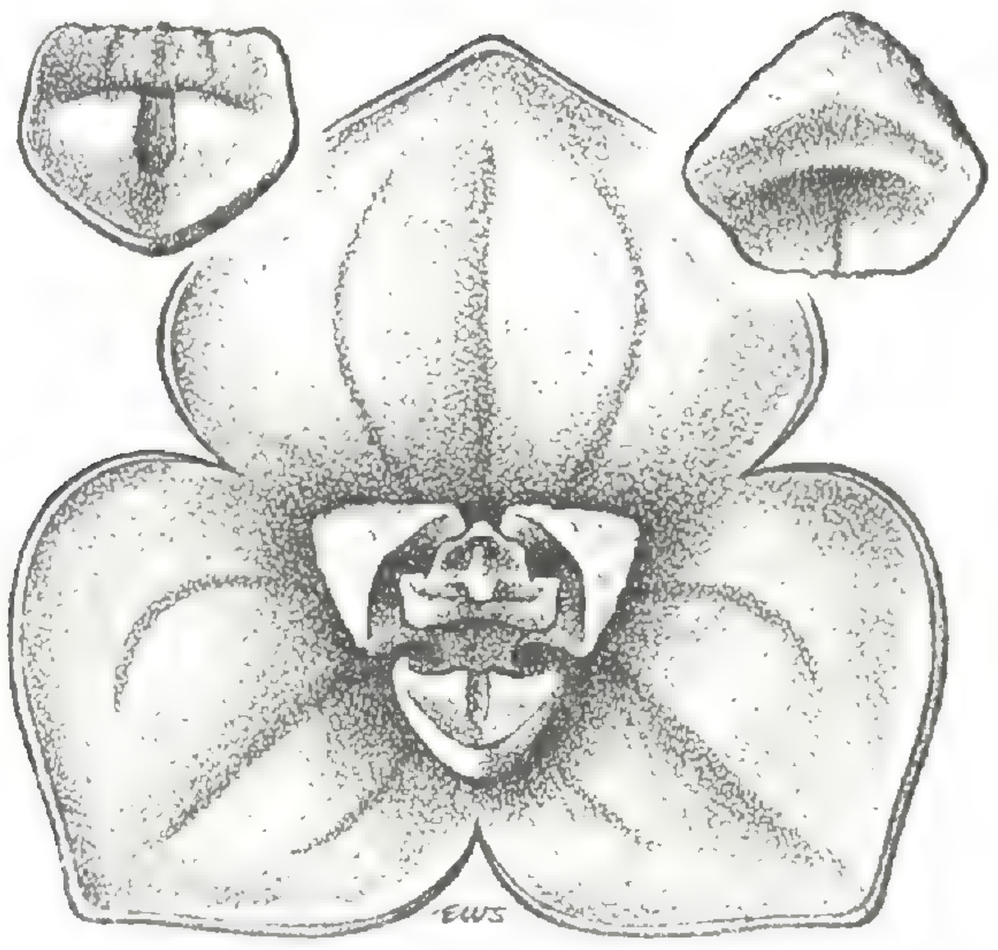
Bolívar: Chimantá Massif, elfin forest formation on plateau of southeast-facing upper shoulder of Apácara-tepuí, at 2000 meters altitude, "epiphyte on branch; leaves fleshy-coriaceous, pale green; scape brown-purple as are the pedicels; calyx [sepals] copper-brick with tawny-yellow margins," June 19, 1953, *Julian A. Steyermark 75712* (Type in Herb. Ames No. 69505).

Stelis obovata *C. Schweinfurth sp. nov.*

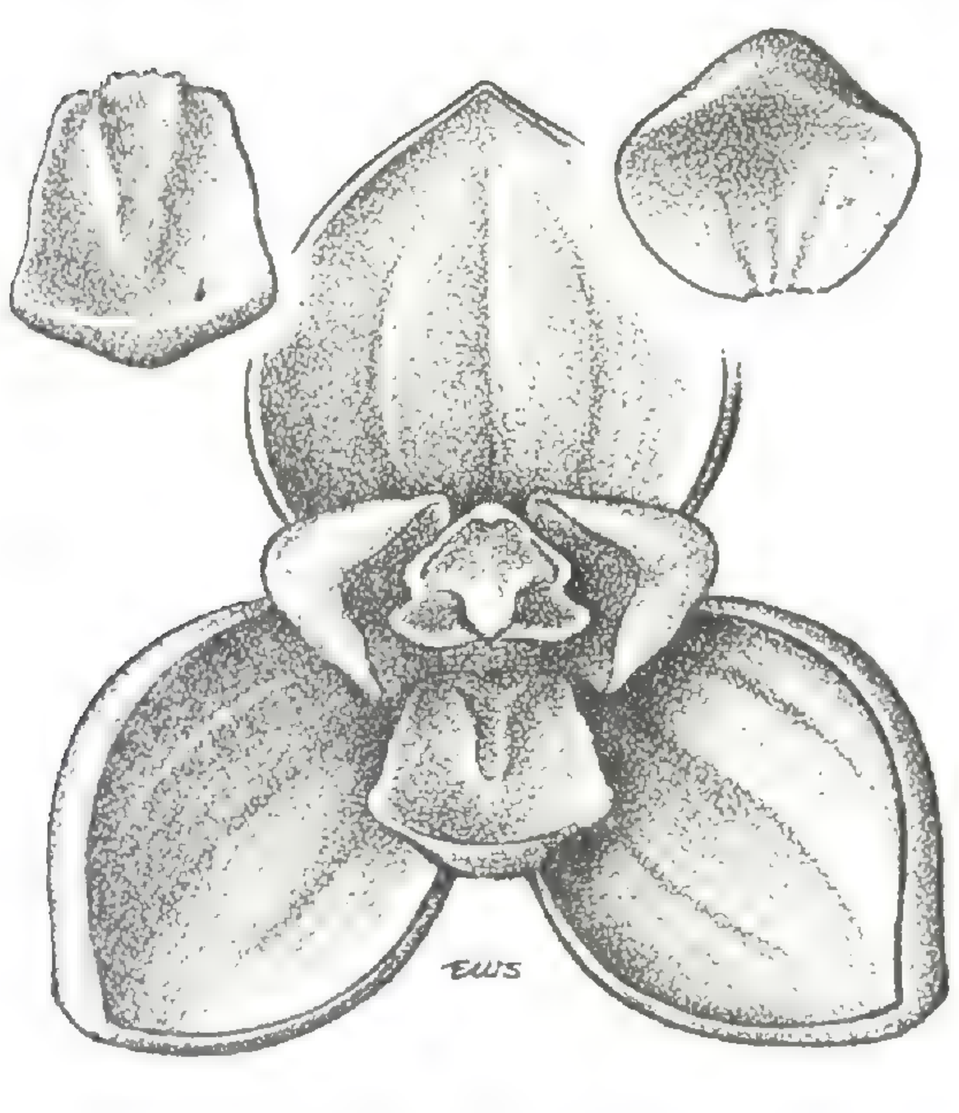
Herba parvula, caespitosa, epiphytica, usque ad 12 cm. alta. Caules approximati, breves, usque ad 1.3 cm. alti, bivaginati, vaginis arctis, tubulatis obtecti. Folium erectum, spathulatum vel oblanceolatum (raro obovatum), apice saepissime obtusum vel rotundatum, usque ad 2.8 cm. longum et 9 mm. latum. Inflorescentiae folium multo superantes, usque ad 10.3 cm. longae; racemus superne dense multiflorus, saepe secundus. Flores minuti, carnosiores. Sepala rotundato-ovata, obtusa vel subacuta, concava, trinervia, subaequalia, basi paulo connata, lateralia obliqua. Sepalum dorsale circiter 2 mm. longum et 1.8 mm. latum. Petala multo minora, in positu naturali cuneato-obovata, circiter 0.8 mm. longa et fere lata, parte superiore carnosissima. Labellum simplex, cuneato-obovatum, apice subtruncatum et incrassatum, circiter 1 mm. longum et latum; discus medio cum callo lanceolato-pandurato. Columna generis, minuta, supra abrupte dilatata.

This species appears to be closely allied to *Stelis lentiginosa* Lindl., the peculiar lip being almost identical,

Plate XXIX



Stelis latisepala *C. Schweinfurth*
Flower expanded, lip and petal, all much enlarged.



Stelis obovata *C. Schweinfurth*
Flower expanded, lip and petal, all much enlarged.
Drawn by Elmer W. Smith

but it differs in having a caespitose habit of growth and much smaller flowers.

AMAZONAS: Cerro Huachamacari, Río Cunucunuma, epiphytic in cumbre near Summit Camp, at 1800 meters altitude, flowers cream-colored, December 14, 1950, *Bassett Maguire, R. S. Cowan & John J. Wurdack 30204.* (This collection differs from the type in its much smaller vegetative proportions and somewhat smaller flowers.) BOLÍVAR: Chimantá Massif, Central Section, on rocky slopes of zanjon bordering Upper Falls of Río Tirica above Summit Camp, at 1950 meters altitude, "epiphyte on mossy branch, lvs. coriaceous, pale green; peduncle and pedicels pale green; fls. greenish yellow," February 7, 1955, *Julian A. Steyermark & John J. Wurdack 556* (TYPE in Herb. N.Y. Botanical Garden).

Octomeria cordilabia *C. Schweinfurth sp. nov.*

Herba valde variabilis, caespitosa, terrestris vel epiphytica. Caules pergraciles, elongati, usque ad 37 cm. alti, multiarticulati, vaginis longe tubularibus arctissimis omnino velati. Folium lanceolato-lineare, sessile, apice minute et oblique bilobatum, crasse coriaceum, usque ad 6.6 cm. longum et circiter 5 mm. latum. Flores in folii axilla fasciculati, parvi, aurei vel aurantiaci, membranacei. Sepalum dorsale late elliptico-ovatum, subacutum, saepissime trinervium, usque ad 5.2 mm. longum et 4 mm. latum. Sepala lateralia breviora et latiora, orbiculari-ovata, saepissime trinervia, usque ad 4.3 mm. longa et 4.1 mm. lata. Petala late ovato-elliptica, subacuta, trinervia, usque ad 4.1 mm. longa et 3.4 mm. lata. Labellum segmentis ceteris multo minus, suborbiculari-ovatum, antice late rotundatum et minute apiculatum, basi cordatum, usque ad 1.7 mm. longum et 2.4 mm. latum; discus callis binis carnosis convergentibus ornatus. Columna parva, arcuata, basi apiceque dilatata.

This species does not appear at present to have any close allies. The relatively long stems, small leaves and entire lip are distinctive.

AMAZONAS: Cerro Huachamacari, Río Cunucunuma, between Summit Camp and "East Ridge" savanna, at 1800 meters altitude, in

densely wooded valley, December 8, 1950, *Bassett Maguire, R. S. Cowan & John J. Wurdack 30035;* Cerro de la Neblina, Río Yatua, near Cumbre Camp, in scrub forest along runlet, at 1700 meters altitude, on rocks and tree trunks, January 5, 1954, *Bassett Maguire, John J. Wurdack & George S. Bunting 37067;* Same locality, along escarpment west of Cumbre Camp, at 1700–1800 meters altitude, occasional terrestrial, *Maguire, Wurdack & Bunting 37099;* Same locality, on Caño Grande slopes, east of Cumbre Camp, at 1600–1800 meters altitude, on limb of low tree, November 22, 1957, *Bassett Maguire, John J. Wurdack & Celia K. Maguire 42183;* Same locality, near Cumbre Camp, at 1800 meters altitude, occasional terrestrial in scrub forest, November 29, 1957, *Maguire, Wurdack & Maguire 42258* (TYPE in Herb. N.Y. Botanical Garden).

Octomeria dentifera *C. Schweinfurth sp. nov.*

Herba parva, caespitosa, saxicola, usque ad 14 cm. alta. Caules graciles, breves, pauciarticulati, 5–8 cm. alti, vaginis longe tubulatis maxima pro parte obtecti. Folium erectum, lineari-lanceolatum vel elliptico-lineare, acutum, sessile, crasse coriaceum, 3.5–6.7 cm. longum, usque ad 6 mm. latum. Flores bini ut videtur, axillares, pro planta magni, membranacei. Sepala similia, trinervia, lanceolata, 10.5–11 mm. longa. Sepalum dorsale acuminatum, usque ad 4.2 mm. latum. Sepala lateralia paulo angustiora, leviter obliqua, longe acuminata, usque ad 3.5 mm. lata. Petala sepalo dorsali similia, ovato-lanceolata vel elliptico-lanceolata, acuminata, usque ad 10 mm. longa et 3.7 mm. lata. Labellum segmentis ceteris multo minus, in positu naturali oblongo-ellipticum et 5.4 mm. longum, infra medium trilobatum cum lobis lateralibus parvis auriculiformibus erectis et lobo intermedio comparate magno, oblongo-ovato, antice subtruncato, marginibus irregulariter dentatis; discus in medio cum carinis binis carnosis. Columna gracilis, arcuata, circiter 4 mm. alta, in pedem conspicuum producta.

This species is allied to *Octomeria parvula* C. Schweinf., but is larger throughout with the flower nearly twice as

large. The specific name is in allusion to the dentate margins of the lip.

Bolívar: Churu-tepuí (Muru-tepuí), northwest cumbres, occasional on rock ledges in upper cumbre, at 2250–2300 meters altitude, flowers white, January 26, 1953, *John J. Wurdack 34218* (Type in Herb. Ames No. 69525); Chimantá Massif, east central portion of summit of Apácara-tepuí, at 2450–2500 meters altitude, "on moist ledges of high large rock around cave recess, leaves dark purple or dull green with purple; pedicels reddish; sepals, petals and lip pale yellow, nodding," June 21–22, 1953, *Julian A. Steyermark 75867*.

Octomeria filifolia *C. Schweinfurth sp. nov.*

Herba gracillima, epiphytica, caespitosa, usque ad 17 cm. alta. Caules tenues, pluriarticulati, circiter 3.5–9 cm. alti, vaginis longe tubulatis arctissimis celati. Folium angustissime lineare vel filiforme, in vivo subteres, usque ad 9 cm. longum et in sicco 1.5 mm. latum. Flores in glomerulis axillaribus, minimi, membranacei. Sepala trinervia. Sepalum dorsale oblongo-lanceolatum, acutum vel acuminatum, tubulari-involutum, circiter 3 mm. longum et 1 mm. latum expansum. Sepala lateralia triangulari-lanceolata, acuta, cum pede mentum formantia, circiter 3 mm. longa et 1.2 mm. lata. Petala lanceolata-linearia, acuta vel acuminata, tubulari-involuta, 1-nervia, sepalis paulo breviora, circiter 2.4 mm. longa et 0.6 mm. lata. Labellum parvum, tubulari-involutum, prope medium trilobatum, basi cuneatum, expansum circiter 1.5 mm. longum et fere 1 mm. latum; lobi laterales oblique semiovati, acuti; lobus intermedius multo major, suborbicularis, apice rotundatus et minute apiculatus; discus lobi medii basi obscure bicarinatus. Columna antice plana, circiter 1.4 mm. alta.

No close ally of this species was noted.

Bolívar: Chimantá Massif, northwestern part of Abácapa-tepuí, vicinity of Camp 3, at 1300 meters altitude, on forested slopes adjacent to quebrada, epiphyte on tree trunk, "leaves purplish with green; petiole purple; flowers pale green with lavender," April 20, 1953, *Julian A. Steyermark 75181* (Type in Herb. Ames No. 69526).

Octomeria flaviflora *C. Schweinfurth sp. nov.*

Herba elata, caespitosa, terrestris. Caules pluriarticulati, usque ad 47 cm. alti, vaginis longe tubulatis marcescentibus maxima pro parte obtecti. Folium erectum, lineari-oblongum, apice minute tridenticulatum, basi sessile, valde coriaceum, usque ad 18 cm. longum et 1.4 cm. latum. Flores numerosi, in glomerulis axillaribus, flavi, membranacei, cum segmentis patentibus. Sepala petalaque lanceolata, acuminata, trinervia. Sepalum dorsale longe acuminatum, 8–11 mm. longum, 3–3.5 mm. latum. Sepala lateralia simillima, paulo obliqua, 8–11 mm. longa, 2.2–3.1 mm. lata. Petala paulo breviora, ovato-lanceolata, saepissime latiora, circiter 7–9.2 mm. longa, usque ad 4 mm. lata. Labellum segmentis ceteris multo minus, in circuitu ovato-oblongum, usque ad 5 mm. longum et 3 mm. latum, prope basim trilobatum; lobi laterales perparvi, anguste falcato-oblongi; lobus intermedius comparate magnus, oblongo-ovatus, apice saepissime subtruncatus et medio acutus, cum marginibus denticulato-erosis; discus callis binis humilibus ornatus. Columna parva, arcuata, usque ad 3–4 mm. alta, in pedem brevem producta.

Amazonas: Cerro de la Neblina, Río Yatua, at 2000 meters altitude, locally frequent in rocky ravine 16 kilometers southwest of Cumbre Camp, December 1–2, 1957, *Bassett Maguire, John J. Wurdack & Celia K. Maguire 42280;* Same locality, at 1900–2000 meters altitude, locally frequent in upper Cañon Grande basin above Salto Grande, December 13, 1957, *Maguire, Wurdack & Maguire 42362;* Cerro Sipapo (Paráque), at 1600 meters altitude, occasional along streambanks in Caño Profundo, January 12, 1949, *Bassett Maguire & Louis Politi 28315;* Cerro Huachamacari, Rio Cunucunuma, at 1800 meters altitude, occasional on left bank of Caño de Dios in cumbre near Summit Camp, December 6, 1950, *Bassett Maguire, R. S. Cowan & John J. Wurdack 30024* (Type in Herb. Ames No. 69523); Same locality and altitude, locally frequent in dense woodland in cumbre along right fork of Caño de Dios near Summit Camp, December 13, 1950, *Maguire, Cowan & Wurdack 30194.* Bolívar: Cerro Guaiquinima, Río Paragua, at 1500 meters altitude, occasional in open savanna on precipitous slope below west

EXPLANATION OF THE ILLUSTRATION

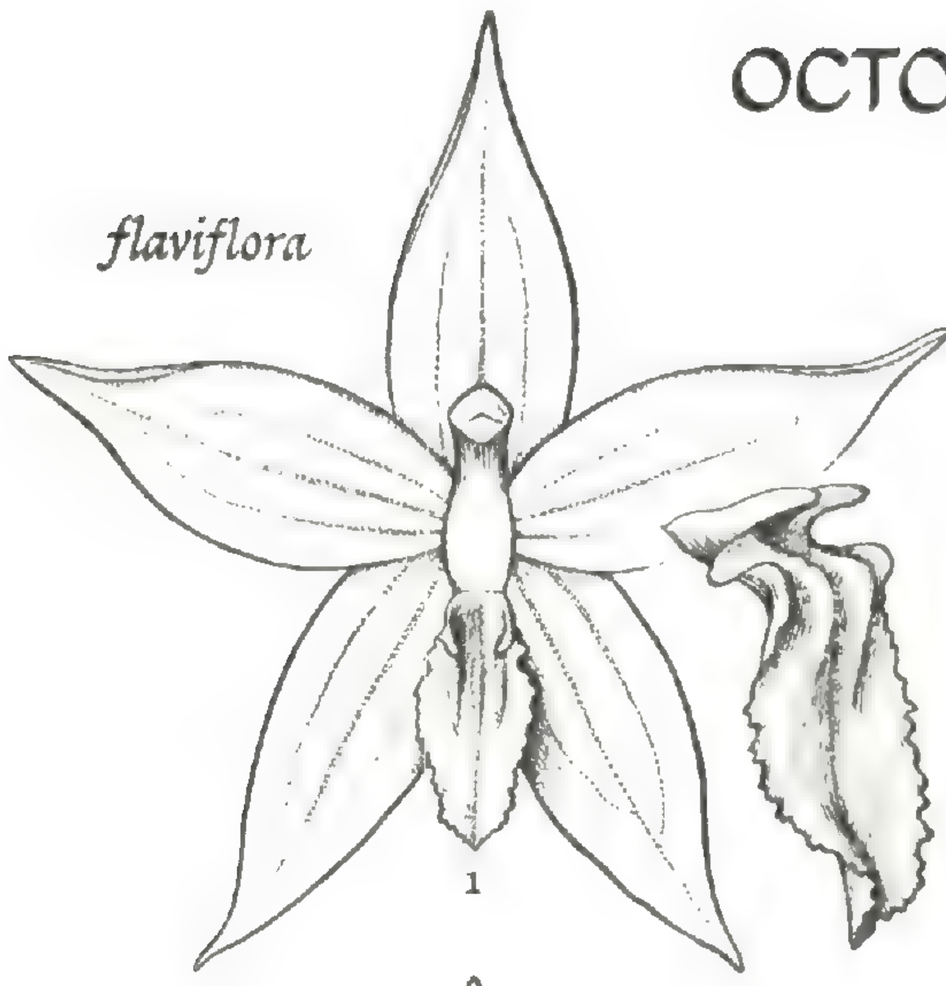
PLATE XXX. OCTOMERIA. 1, O. FLAVIFLORA *C. Schweinfurth*. Flower expanded, three times natural size. Lip, three quarters view, five and one half times natural size. 2, O. NANA *C. Schweinfurth*. Flower expanded, eight times natural size. Lip, three quarters view, eleven times natural size. 3, O. DENTIFERA *C. Schweinfurth*. Flower expanded, two and one half times natural size. Lip, three quarters view, four and one half times natural size. 4, O. LANCIPETALA *C. Schweinfurth*. Flower expanded, five and one half times natural size. Lip, three quarters view, twelve times natural size. 5, O. FILIFOLIA *C. Schweinfurth*. Flower expanded, nine times natural size. Lip, three quarters view, twenty-two times natural size. 6, O. CORDILABIA *C. Schweinfurth*. Flower expanded, five and one half times natural size. Lip, three quarters view, twelve times natural size.

Drawn by ELMER W. SMITH

Plate XXX

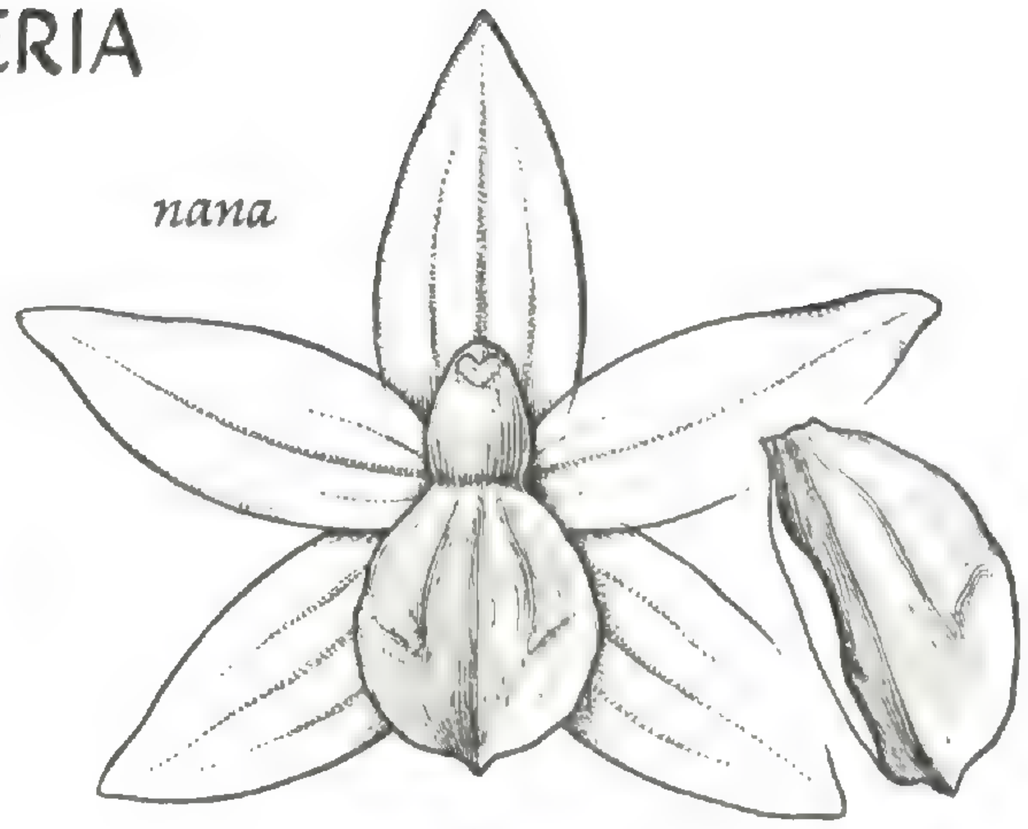
OCTOMERIA

flaviflora



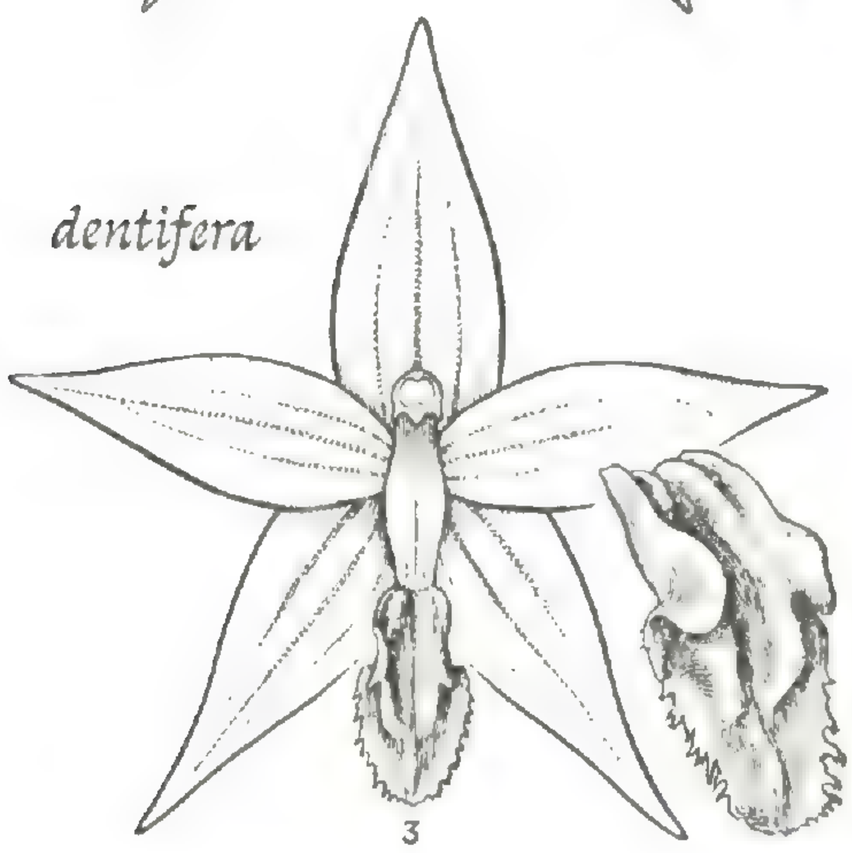
1

nana



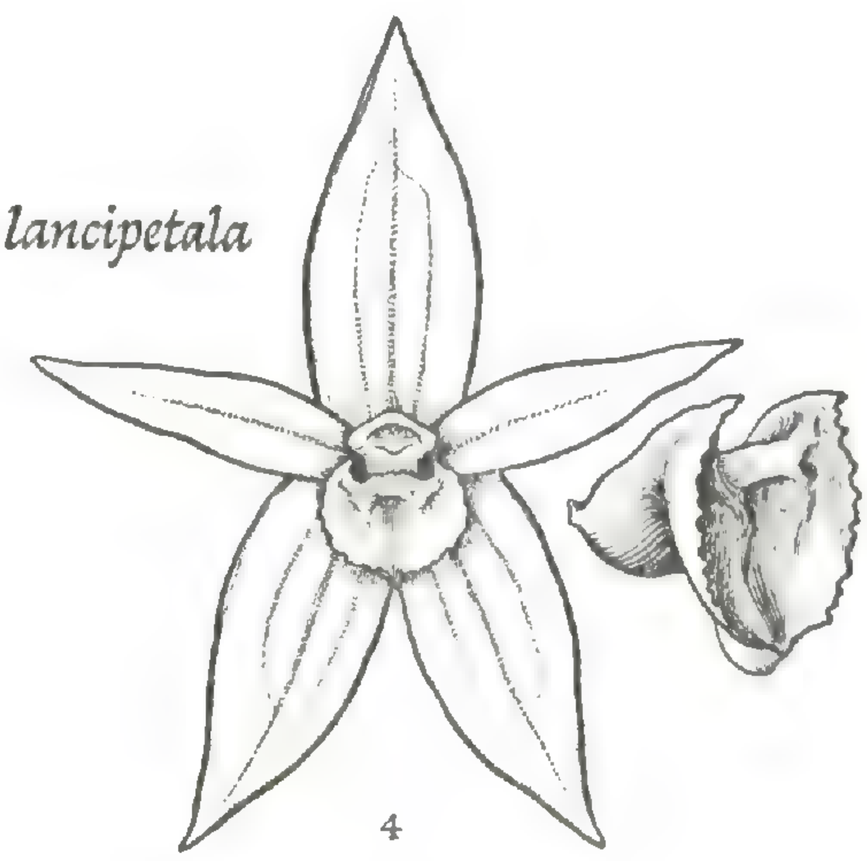
2

dentifera



3

lancipetala

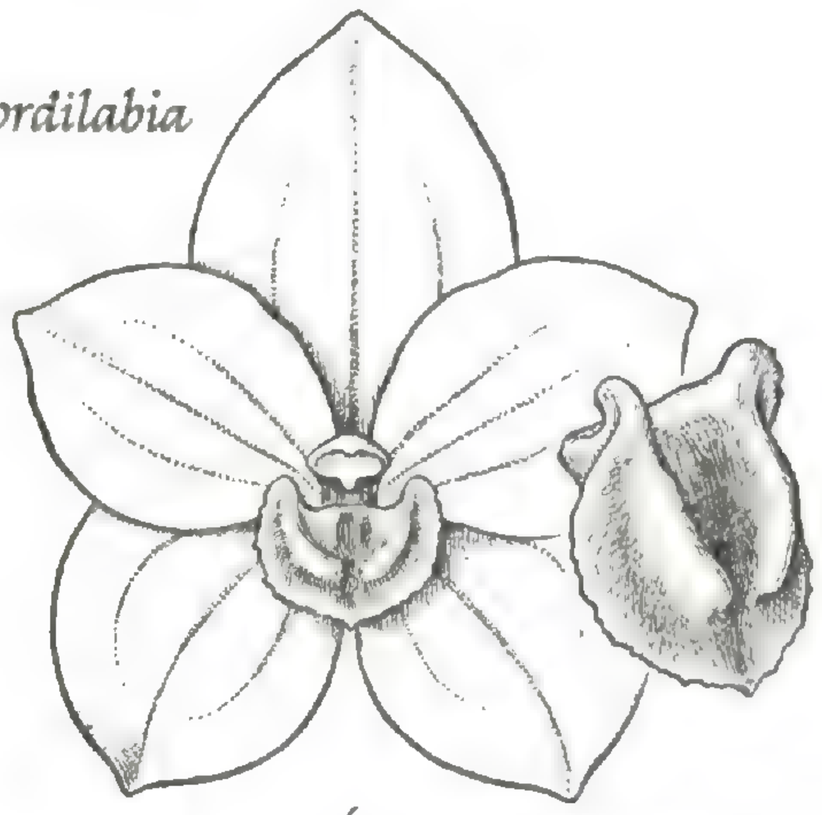


4

filifolia

5

cordilabia



6

E.W. Smith

escarpment, December 31, 1951, *B. Maguire 32877;* Chimantá Massif (Central Section), at 1940 meters altitude, on border of large rocks by large savanna below Upper Falls of Río Tirica above Summit Camp, "sepals yellow with dull brick-red margins and tips; lip maroon; column greenish with pale yellow apex," February 7, 1955, *Julian A. Steyermark & John J. Wurdack 607.*

Octomeria lancipetala *C. Schweinfurth sp. nov.*

Herba parva vel mediocris, epiphytica. Caules graciles, usque ad 17.5 cm. alti, pluri- vel multiarticulati, vaginis longe tubularibus arctissime celati. Folium lanceolato-lineare, apice acutum vel minute tridenticulatum, crasse coriaceum, circiter usque ad 9 cm. longum et 4.5 mm. latum. Flores parvi, numerosi, in glomerulis axillaribus, cum segmentis patentibus. Sepalum dorsale ovatum vel lanceolato-ovatum, acutum vel acuminatum, trinervium, circiter 4 mm. longum et 2.1 mm. latum. Sepala lateralia similia, sed paulo longiora et angustiora. Petala anguste lanceolata, acuta vel acuminata, uninervia, circiter 3.2–3.8 mm. longa et 1 mm. lata. Labellum segmentis ceteris multo minus, simplex, valde geniculatum, antice late rotundatum et aliquando apiculatum, postice cordato-truncatum, circiter 1.1 mm. longum et 1.5–1.8 mm. latum, cum ungue brevi cuneato; discus basi incrassatione obliqua utrinque ornatus. Columna minuta, crassa, apice dilatata, circiter 1 mm. alta.

This species appears to be allied to *Octomeria cordilabia* C. Schweinf., but has commonly much shorter stems and very dissimilar sepals and petals.

Amazonas: Cerro Huachamacari, Río Cunucunuma, frequent in cumbre, at 1700 meters altitude, flowers purple, December 4, 1950, *Bassett Maguire, R. S. Cowan & John J. Wurdack 29823;* Same locality, along right fork of Caño de Dios near Summit Camp, at 1800 meters altitude, in dense woodland, December 13, 1950, *Maguire, Cowan & Wurdack 30170A* (Type in Herb. Ames No. 69528); Cerro de la Neblina, Rio Yatua, in scrub forest 1 to 5 kilometers north of Cumbre Camp, at 1800 meters altitude, occasional on tree trunks, buds maroon, January 10, 1954, *Bassett Maguire, John J. Wurdack & George*

S. Bunting 37161; Same locality, in swale 2 kilometers northeast of Cumbre Camp, at 1800 meters altitude, on limb of low tree, flowers maroon, November 20, 1957, *Bassett Maguire, John J. Wurdack & Celia K. Maguire 42150.*

Octomeria nana *C. Schweinfurth sp. nov.*

Herba pusilla, caespitosa, rupicola, usque ad 4 cm. alta. Caules brevissimi, usque ad 13 mm. alti, circiter 2-articulati, vaginis tubulatis marcescentibus celati. Folium oblongo-lineare, valde carnoso-coriaceum et per medium sulcatum, acutum, sessile, usque ad circiter 23 mm. longum et 2 mm. latum in sicco. Flores axillares, pauci, glomerati, membranacei. Sepala similia, prope basim trinervia. Sepalum dorsale ovato-oblongum, acutum, concavum, circiter 3.7 mm. longum et 1.5 mm. latum. Sepala lateralia oblique ovato-oblonga, acuta, circiter 3.5 mm. longa et 1.5 mm. lata. Petala oblique oblongo-lanceolata, concava, subacuta, circiter 3.5 mm. longa et 1.2 mm. lata, maxima pro parte uninervia. Labellum segmentis ceteris multo brevius, simplex, suborbiculare, antice rotundatum et apice abrupte acuto, ad basim rotundatam angustatum, trinervium, circiter 2.2 mm. longum et 2 mm. latum; discus in medio obscure bicallosus. Columna minuta, crassa.

This dwarf species seems to have no near allies. The only available flowers occurred at the summit of enlarged, ellipsoid ovaries.

Bolívar: Chimantá Massif, Torono-tepuí, north-facing slopes on summit above Caño Mojado, on rock in savanna, at 2030–2150 meters altitude, "lvs. 3–4 mm. thick," February 21, 1955, *Julian A. Steyermark and John J. Wurdack 1027* (Type in Herb. Ames No. 69524).

Ponthieva ovatilabia *C. Schweinfurth sp. nov.*

Herba terrestris, elata, usque ad 87 cm. alta. Radices fasciculatae, fibrosae, lanuginosae. Folia plura, in herbae basi, longe petiolata; lamina ovato-lanceolata vel elliptico-lanceolata, acuminata, basi cuneata, membranacea, tri-

EXPLANATION OF THE ILLUSTRATION

PLATE XXXI. PONTHIEVA OVATILABIA *C. Schweinfurth.* 1, plant, one half natural size. 2, flower expanded, with lip and column foreshortened, five times natural size. 3, lip expanded, six times natural size.

Drawn by ELMER W. SMITH

Plate XXXI

nervia, 7–13 cm. longa, usque ad 3.8 cm. lata; petiolus canaliculatus, satis gracilis, circiter 5–10 cm. longus. Caulis glanduloso-pilosus, usque ad inflorescentiam circiter 59.6–71.4 cm. altus, vaginis pluribus remotis ornatus. Racemus laxe multiflorus, cum rhachide circiter 10–16 cm. alta. Flores parvi, viridi-albidi. Sepala extus sparse glanduloso-pilosa. Sepalum dorsale elliptico-lanceolatum, ad apicem subacutum angustatum, trinervium, 6–7 mm. longum, circiter 2 mm. latum. Sepala lateralia oblique ovata, subacuta, 6–7 mm. longa, circiter 3.1–3.4 mm. lata, quinquenervia. Petala unguiculata; lamina obliquissime triangularis, acuta, basi semicordata, circiter 4.7 mm. longa et 3 mm. lata; unguis oblongo-linearis, carnosus, circiter 1.3 mm. longus. Labellum columnae parti superiori adnatum, valde inflexum, cum lateribus involutis, expansum in circuitu ovatum, circiter 4 mm. longum et inferne 2.3 mm. latum, parte anteriore oblongo-lineari et parte posteriore suborbiculari; discus basi cum callo rotundato-hippocrepiformi. Columna perbrevis, crassa, supra abrupte dilatata, circiter 2.5 mm. alta.

This species is vegetatively similar to *Ponthieva diptera* Linden & Reichb.f., but the petals and lip are very different. The lip somewhat recalls that of *P. ecuadorensis Schltr.*

AMAZONAS: Cerro de la Neblina, Río Yatua, 700 meters altitude, occasional in *Clusia* scrub forest just south of Camp 3, December 31, 1957, *Bassett Maguire, John J. Wurdack and Celia K. Maguire 42559* (TYPE in Herb. Ames No. 69529). BOLÍVAR: Cerro Venamo, northwest slopes, 1100 meters altitude, terrestrial in moist mossy forest, leaves firmly membranaceous, deep green above, dull gray green beneath, pedicels recurved, nodding, pale green, ovary ivory-white, April 21, 1960, *Julian A. Steyermark & S. Nilsson 431.*

BOTANICAL MUSEUM LEAFLETS
HARVARD UNIVERSITY

CAMBRIDGE, MASSACHUSETTS, MAY 7, 1962 VOL. 19, NO. 10

EDIBLE FRUITS OF SOLANUM IN SOUTH AMERICAN HISTORIC AND GEOGRAPHIC REFERENCES[1]

BY

VICTOR MANUEL PATIÑO[2]

ONE of the imperfectly understood aspects of economic botany in South America seems to be the use of the edible fruits of sundry species of Solanum. Not only is the extent to which long-known species are employed a question; but how many species, some perhaps not yet described, are involved remains for intensive agronomic and taxonomic research to clarify. The history of domestication and geographic dispersal of several of the Solanum-concepts herein considered remains, in some aspects, uncertain. It is hoped that a thorough consideration of historic and geographic reports of these plants may add to our growing understanding of them.

Solanum quitoense *Lamarck* Illustr. 2 (1797) 16.

VERNACULAR NAMES:

Lulo in western Colombia.

[1] This article is part of a work on the history of cultivated plants in equinoctial America which I have been preparing with the help of the John Simon Guggenheim Memorial Foundation and OAS Fellowship Program. The research has been done mainly in the Library of Congress, Washington, D.C. and the Botanical Museum of Harvard University, Cambridge, Mass.

[2] Formerly Chief of Colonial Crops, Secretariat of Agriculture, Cauca Valley, Colombia.

Ma-sha-kvé in Kamsá or Koche, Sibundoy, Colombia (Schultes, 1949, 45).

Naranjilla in Ecuador, southernmost Colombia.

The few authors who have been concerned with this fruit agree that the word *lulo* is of Keshwa origin. Some linguists attribute it to the Quitoan or northernmost form of *ruru*, meaning "egg," "fruit" (Lira, 1945, 557; Toscano Mateus, 1953, 93). The earliest known Keshwa-Spanish vocabulary states of *llullu:* "unripe thing: soft bud of tree or anything similar" (Domingo de Santo Tomás, 1560, 147). Another Keshwa vocabulary of the beginning of the 17th Century reports: "*llullu-ruru*, everything that is tender before becoming hard"; and "*llullu-ruru*=tender, milky fruit" (González Holguín, 1608, 213; González Holguín, 1952 (ed. fascim.)). The first reported name which was applied to a solanaceous plant with a description corresponding reasonably to *Solanum* aff. *quitoense* Lam. is *puscolulu*, derived, as suspected by Jiménez de la Espada (see below), from *ppochcco-ruru:* "sour or acid fruit." González Holguín, in fact, says: "*pochcco*=yeast or thing acid or sour" (González Holguín, 1608, 295). Theoretically, it could also be accepted that *puscolulo* means "mucilaginous fruit," from "*puçoco*="foam or slaver" (Domingo de Santo Tomás, 1560, 162 v.).

While we admit that *lulo* is of Keshwa origin, it is not clear how the term *pusco* has disappeared from *puscolulo*, whereas the names of several other fruits have kept it: e.g., *asna-lulo* and *chaqui-lulo*, quoted by some colonial sources for fruits from the highlands of the Province of Pasto; and *chonta-ruro*, a name known since the end of the 16th Century (Patiño, 1958, AI, XVIII, 177–204; 299–332).

Since *Solanum quitoense* is indigenous to the equinoctial region, one may justifiably assume that the name

lulo belonged to a local language. In the Kolorado language, formerly spoken on the coast and western Andean slope of Ecuador, the root *lu* refers to "red" and "yellow" and, as a natural extension, "ripeness" (Jijón y Caamaño, 1941, II, 249). The repetition *lulo* should indicate, as stated by Buchwald, "red, red" (ibid., 250). There is a river in that same region, the Río Lulo, a tributary of the Palenque (Wolf, 1892, 138).

In Kamsá and its filial tongue Koayker, the particle *sha* (*thsa*, *za*, *scha*, *cha*) is equivalent to "thing good, admirable" and serves to classify the fleshy objects (Jijón y Caamaño, 1940, I, 102–103, 105, 107, 109, 117–120, 122–124; 157, 160, 191–192). In Kamsá, *be* means "round" (ibid., 118, 122).

The origin of the word *naranjilla* is established in the references quoted below. In view of the lack of botanical collections, some of the data on several so-called varieties of naranjilla (Gattoni, 1935, 7) may refer perhaps to different species. A few years ago, Schultes and Cuatrecasas described a variety of *Solanum quitoense*[3] occurring north of the equator and characterized by the presence of spines on the leaves.

In 1652, the naturalist Bernabé Cobo, perhaps making use of information sent to him by Jesuit correspondents, described under different regional names one or more species of Solanum with edible fruits, native of the regions of Popayán and Quito. Living in Lima and Mexico, Padre Cobo was never able to visit these two regions. The descriptions are alike, except in a few details which are easily detected by reading the references in double column as follows:

[3] **Solanum quitoense** *Lamarck* var. **septentrionale** *Schultes & Cuatrecasas* in Bot. Mus. Leafl. Harvard Univ. 16 (1953) 100.

Chapter XVI
ON PUSCOLULO

In the Province of Popayán, there grows a bush called *puscolulo*,[4] which is like hell's-little-fig in size, leaf and shape. It bears a fruit very similar to an apple in size, colour and rind; but it is covered all over with tiny spines (hairs) which easily rub off. The flesh is between green and yellow, watery, and full of little seeds like those of the pepper; they are eaten together with the flesh. The flavor tends more to sour than to sweet, and eating too many [fruits] sets the teeth on edge'' (Cobo, 1890, I, 461; Cobo, 1956, I, 209–210).

Chapter XXIII
ON THE NARANJILLAS

In the Province of Quito, there grows a bush more or less as tall as a man; its leaf is like that of hell's-little-fig, a little larger and spiny along the veins. The fruit which it bears is called naranjillas (''little oranges''), because of a resemblance to oranges. It is of the size of a medium-sized peach, round, orange-coloured; the rind and core are like those of the tomato; the inside is of a watery, bittersweet consistency; it has many little seeds, like the tomato,and of good taste''(Cobo, 1890, 1, 470; Cobo, 1956, I, 213).

Both descriptions agree that the leaves are sinuate, since they are compared with those of ''hell's-little-fig,'' the colonial Spanish name for *Ricinus communis* L. But, while the fruit of puscolulo is said to be covered with spine-like hairs, naranjilla is described as having a smooth fruit like the tomato. Another difference is the presence of spines on the veins of the leaves of naranjilla, a character not mentioned for puscolulo.

From the references given above, it appears that, by the middle of the 17th Century, there were known in Popayán and Quito solanaceous plants with edible fruits which differed both in names and morphological characteristics. Apparently, Cobo did not notice (or at least he fails to mention it) the affinities of the two plants which he described. The same observation can be made in the case of other plants from regions far away from his resi-

[4] Perhaps this must be read *ppochcco*, ''fruit sour or acid,'' in Quíchua, which is, I believe, the ''naranjita de Quito.'' (*Note* by the editor Marcos Jiménez de la Espada.)

dence, and which he described on the basis of reports from other persons.

The Ecuadorian Jesuit, Juan de Velasco, describing the *naranjilla* in 1789, adds nothing new or notable but reports that the leaf is "broad, rough and somewhat spinous" (Velasco, 1927, I, 73–74).

The last two records refer to the interandean equinoctial area from Loja to Popayán. The next two concern the Amazon slope.

The Jesuit, Jean Magnin (1740), includes naranjas and naranjillas without explanation amongst the cultivated fruits of the Province of Maynas (Magnin, 1940, 156).

During the decade of 1760, the Majorcan missionary, Fr. Juan de Santa Gertrudis Serra, lived and worked in the upper part of the Putumayo and Caquetá Rivers. Speaking of the former mission at Santa Rosa de Caquetá, he said: "There is in Santa Rosa an orchard with its fence; inside it, the third part is planted to naranjillas. This is a bush of a man's height, with big leaves, similar to those of egg-plant. But above the leaves have spines, thick and long as a half pin, 15 to 20 on every leaf. It bears fruit at the middle of the plant. Perhaps its resemblance to the orange is why it is called *naranjillas*. They are half the size of oranges and covered with tiny, very thin and pointed spines, so thickly crowded that the fruit looks like velvet. When the fruits ripen, the spines decay, and the naranjilla assumes a very deep scarlet color. The rind is very thin and inside there is no pip. It is like an orange without sections, being entirely a pulp. The color is between green and orange-colored, and the taste bitter-sweet, very appetitious. The fruit is very fresh to the body, and diluted some of them in water with sugar, makes a refreshing drink of which I may say that it is the most delicious that I have tasted in the world" (Serra, 1956, I, 148–149).[5]

The data of the middle of the 17th Century confine the range of puscolulo and naranjilla to the Provinces of Popayán and Quito. Those of the middle of the 18th Century quoted above are restricted to naranjilla; they place its area of cultivation to the east, yet it still falls within the equatorial belt. But the references to be considered below indicate that cultivated *Solanum quitoense* (or some other species mistaken for it) had migrated from the original focus, both to the north and to the south.

In the year 1701, Fr. Alonso de Zamora, writing on the plants of the New Kingdom of Grenada, stated: "There are growing in the hot parts of the country some trees of the stature of lemon trees, called *lulos*. These give a fruit like small oranges and with the same color as oranges; their skin is very thin, and they are very agreeably scented, moderately sour and with numerous seeds inside a soft pulp. This fruit, diluted, is, according to Doctor Lugo, very wise physician who had been in this New Kingdom, a healthy cordial for those sick with typhus (*tabardillo*) and other fevers. Sauces made with this fruit are the most seasoned that the culinary art has discovered" (Zamora, 1701, 41: Zamora, 1930, 40). The Gongorist style of that time did not contribute towards accuracy of description. In this case, the name *lulo* seems to have been borrowed from the western part of New Grenada, but the quotation might equally well be attributed to *Solanum Topiro* (see below) or other species, because it refers the plant to the "hot parts of the country." Some records indicate that in the Guaviare River basin there is a lulo with a fruit larger than that of the

[5] Since *Solanum quitoense* does not normally grow well in hot areas, and since the plant in the foregoing description was said to have spiny leaves, it is possible that this *naranjilla* is referable to a new species, *Solanum georgicum*, described from the same region by Schultes.

lulo from western Colombia.[6] Only field research and the assembling of enough botanical samples will settle the question of what species of Solanum this may be.

In a descriptive report on the District of Vijes in the jurisdiction of Cali, made by José Lorenzo de Reina on July 20th, 1808, we find a statement that the few inhabitants of Ciénaga Larga, in the basin of the Bitaco River, tributary of the Dagua, a temperate region, grew plantains, maize, some arracachas and lulos (Villaquirán, 1959, 61–66 : 232). These lulos are undoubtedly *Solanum quitoense*, most probably the variety *septentrionale*. By the middle of the 18th Century, *Solanum quitoense* had spread to the south. Amongst the plants which he had collected in Lima and vicinity and in the neighboring valleys in the first half of 1778, the botanist Hipólito Ruíz includes: "*Solanum angulosum*, common name *narangitas de Quito*, 'little oranges from Quito,' because they come from that province and because the fruit has the shape and color of a small orange. Women esteem this fruit for its scent and for the particular taste that they give to the maté beverage, the custom being to drop it in some of the juice. They are also accustomed to include these fruits in the mixed bouquets of flowers for the purpose of beautifying the bouquet and of making the mixture more pleasant with its fragrance" (Ruíz, 1952, I, 30). In another place, Ruíz wrote that he sent to Spain seeds of *Solanum peruvianum* or naranjitas de Quito with the first parcel of plants and seeds mailed in 1780. The cases with the living plants were lost (ibid., 434, 443).

In the National Period (the previous data are from Colonial documents), Edouard André saw naranjilla in the Pasto market in 1876 and identified it as *Solanum galeatum*. Although he did not describe the plant, he praised

[6] Verbal report from the agronomist Dr. Camilo Castro, at present Governor of the Department of Meta.

the fruit (André, 1879, 20. sem. XXXVIII, 322). Cárdenas supports the opinion that lulo is a species on the way to domestication, of recent status as a cultigen; and, in some ways, still wild (Cárdenas, 1950, 17–18).

In his work on the Keshwa terms used in the Cauca Valley, Leonardo Tascón offers the following references about lulo; they are included here because they establish definitively the presence in that Colombian area of two different, well known and clearly distinguished forms: "*Lulo.* (from *llullu*, soft, tender). Fruit round, flattened, orange-colored, of sour taste, employed for preparing very agreeable refreshing beverages. It is borne by a solanaceous plant with large, purple leaves, spinous the same as the stem, and with white flowers in a bunch; called in botany *Solanum esculentum.* The *dog's lulo*, the rind of which serves to make sweets, is the fruit of another species that differs from the former in the green colour of its leaves" (Tascón, 1934?, 101). The first of these two concepts of *Solanum* would appear to be *S. quitoense* var. *septentrionale.*

The members of the Russian botanical expedition to Colombia in 1925 found lulos in Manizales (Bukasov, 1930, 488).

In the middle of the 19th Century, the physician-geographer Villavicencio remarked upon the excellence of naranjillos grown at Baeza in eastern Ecuador (Villavicencio, 1858, 403).

Under the abbreviated name of *naranji*, there is a cultivated fruit in Ecuador amongst the Jívaro and Canelo Indians (Karsten, 1935, 123, 568; Sarmiento, 1958, 178). Any doubt that the last two references apply to *Solanum Topiro* is dispelled below.

Solanum Topiro *Humboldt & Bonpland ex Dunal*
Sol. gen. aff. syn. (1816) 10.

VERNACULAR NAMES:

Topiro, tupiro, tupiru (Orinoco-Río Negro basin).

Bo-po amongst the Camaratas Indians, Amazonas Territory, Venezuela (Schultes, 1958, 242).

Betáka, in Kubeo, Vaupés River, Colombia; *detwá* in Tatuya, Apaporis River, Colombia (ibid., loc. cit.).

As suggested above, the lulo mentioned by Zamora in 1701 may refer to topiro, from some of the western tributaries of the Orinoco River: this region, if not often visited at that time, at least was not unknown through the activity of missionaries of different religious orders in touch with Bogotá.[7]

The Jesuits from the eastern plains of New Grenada mentioned sundry native fruits that are probably *Solanum Topiro* or related species. Gumilla, using a name perhaps already spread far from its place of origin (as in the case of lulo), lists amongst the wild fruits date palms (in a generic sense, meaning "palms") and "*naranjillas*, of a bittersweet taste and very wholesome; they are of the same color, although something smaller, than ordinary oranges" (Gumilla, 1841, 197; Gumilla, 1944, I, 266; Gumilla, 1955, 174).

During his second survey of the Padamu River, an affluent of the upper Orinoco, in March and April of the year 1760, Apolinar Díez de la Fuente of the staff of the Commission of Boundaries between the Spanish and Portuguese colonies organized a few years before, travelling from Guaharibos Falls as far as the Casiquiare-Orinoco confluence, found a cultivated field (*conuco*), started the year before, in which maize, beans and tupiros were almost mature (Ramos Pérez, 1946, 407). This

[7] Cuatrecasas collected *Solanum Topiro* (No. 7558) along the Guayabero River, 240 m. altitude, November 8, 1939. (Personal communication). The Guayabero and Ariari Rivers are the principal sources of the Guariare. (See footnote 6.)

field had been made by the Indians in three days (Altolaguirre y Duvale, 1908, 310), near the fortress of Buena Guardia, of which, one hundred years later, not a remnant was to be seen (Michelena y Rojas, 1867, 162, 355).

On their trip to the upper Orinoco in 1800, Humboldt and Bonpland found tupiro at San Fernando of Atabapo, the type locality of the material on which the first description of the species was based. Humboldt included *Solanum Topiro* amongst the common plants in the area between the Javitá and Pimichín Rivers (Humboldt, 1942, IV, 178). Making use, probably, of the works of those two authors, Lisandro Alvarado drew up the following description: "*Tupiro. Solanum Topiro.* Shrub with herbaceous, tomentose stem; leaves subovate, acute, sinuate-angulated, unequal at the base, thickly haired above, lightly grey-tomentose below; flowers extra-axillary, aggregate; berries ovate, tetralocular, edible. Blossoming in May. It is called also *tópiro*" (Alvarado, 1953, 345). This form, accented on the antepenult, is given by Tavera Acosta (1954, 218).

In a recent paper, Schultes attributes to *Solanum Topiro* the *cocona* from eastern Peru and mentioned by Fennel and other authors (Schultes, 1958, 231–232; Fennel, 1948, 181–182). Ricardo Latcham, listing several fruit-bearing species used by Amazonian tribes, mentioned—without quoting sources—the "*cocona*, that bears a berry similar to an orange" (Latcham, 1936, 65–66, 72).

The following statement appears on the naranjilla of eastern Ecuador in a recent work: "There are three kinds: the two acid (known in the east under the names of *huevo de tigre* ("puma testicle") and *cocona*, and the other one common with us [in the highlands], bittersweet and very agreeable, especially for beverages, preserves, ices, sherbets, not to mention its use as an edible

fruit, both alone and with sugar. It is so aromatic that just a single fruit is enough to fill a room with pleasant fragrance. The cocona is also a special insecticide, used by the eastern Indians against head-lice. They also eat the fruit roasted'' (Sarmiento, 1958, 178).

In the market of Iquitos, I found for sale in 1951, under the name of *cocona*, and I have eaten there, a berry larger than that of *Solanum quitoense*, with a rind of dark purple or murrey, not orange-colored or yellow. It is possible that, in eastern Peru, the term *cocona* is applied to several species-concepts of Solanum.

Along with other fruits, cocona is grown by the Kareneiris Indians of the upper Madre de Dios River in eastern Peru (Fejos, 1940–1942, 24).

By October 1948, seeds of cocona were introduced from the United States to the Tulio Ospina Farm in Medellín, Colombia. According to official reports, the shrub has but few spines, and the fruits are orange-colored (Granja Tulio Ospina; letter August 1956; letter 329, October 5, 1961).

Solanum muricatum *Aiton* Hort. Kew., ed. 1, 1 (1789) 250.

Solanum muricatum Aiton var. *popayanum* Bitt. (Bukasov, 1930, 530).

VERNACULAR NAMES:

Cachon, in Keshwa (Domingo de Santo Tomás, 1560, 112 v.; Domingo de Santo Tomás, 1951, 242; González Holguín, 1608, 258).

Cachuma, in Aymara (Bertonio, 1612, 32).

Pepino, pepino dulce.

The name *pepino* was given to the fruit by the Spaniards who saw in it some resemblance to the cucurbitaceous cucumber (*Cucumis sativus* L.), which they had introduced into the New World.

Referring to the irrigated Peruvian coastal plains, Cieza de León (1553), described the so-called pepinos as one of the most remarkable of American fruits (Cieza, 1924, 209). While recounting the last campaigns of Huayna Cápac across the northernmost coast of Peru, the same author gives this anecdotal passage: "And it is said about him, that when he was travelling along the beautiful plain of Chayanta, near Chimó, where the city of Trujillo is now built, an old Indian was at work in an agricultural field. Having heard that the king was passing nearby, he took three or four pepinos and, with earth and all, presented them to him, saying: "*Ancha Atunapu micucampa*" ("Great sir, eat thou this"). In the presence of his knights and others, he took the *pepinos* and, tasting one of them, said to gratify the old man: "*Xuylluy, ancha mizqui cay*" ("This is indeed very sweet"). From this act, everybody derived very, very great satisfaction" (Cieza, 1880, 250–251). The expeditions of Huayna Cápac in the Chimú-Mochica region were made after the death of his father, Tupac Inca Yupanqui, towards 1481 (Vázquez de Espinosa, 1948, 541–544). The same Cieza de León, speaking of the Chincha Valley, lauds the beauty of the orchards there "and saw what delightful and fragrant pepinos [there are], not like those from Spain, although in form somewhat alike, for those from this region [of Peru] are yellow when peeled, and so appetizing that, in truth, a man needs to eat many before he loses his taste for them" (Cieza, 1924, 229).

Juan de Salinas Loyola, in his description of Loja, Ecuador, written in Spain in 1571–1572, spoke of these fruits, saying that there is "a native kind of cucumber there." In 1572, in his excellent report on Quito, written likewise in Spain, he is more explicit: "There is another kind of cucumber, which grow like those of

Spain; it is smooth, white, with some murrey veins; the Indians eat it, and it is believed that it is more wholesome than ours, and not so cool." Sancho Páz Ponce de León in his report on Otavalo (1582) claimed that there was the Spanish cucumber and also one "from these parts" in the vicinity of Pizque, along the Guaillabamba River, just as in other places near the Mira or Coangue River (J. de la Espada, 1897, III, 203, 73, 113). Even at the present time, it is the daily custom to sell excellent pepinos to the passengers stopping for a while at the village El Olivar to the north of the city of Ibarra, Imbabura Province, on the road between Quito and Tulcán and Pasto. In the second quarter of the 17th Century, Vázquez de Espinosa, listing the productions of Quito, stated that there are "cucumbers very different and better than ours" (Vázquez de Espinosa, 1942, 363; Vázquez de Espinosa, 1948, 340).

We do not have such early reports for New Grenada. We cannot know whether or not the growing of this species, carried on now as far north as Popayán and even in Antioquia and on the Bogotá plateau, dates from prehispanic times or only since the Conquest. But if the cachon were cultivated in the upper Mira River basin, the southernmost boundary of expansion of the Pastos group, it may be assumed that the cultivation of *Solanum muricatum* had spread northward at least as far as the basin of the river called now Guáitara. Fr. Alonso de Zamora said that at the end of the 17th Century there was in the New Kingdom of Grenada, an abundance of "pepinos" of several kinds, including the sweet one (Zamora, 1701, 45; Zamora, 1930, 43).

In 1590, Acosta reported: "Neither are the so-called pepinos [*Solanum muricatum*] trees, but vegetables that are annual in habit. This name was given to them because some of them, even most of them, are long and

round like the true cucumber; but in everything else they differ sharply, for the color is not green but murrey, yellow or white; they are not spiny or rough, but quite smooth. Their taste is very unlike and very superior, for when they are wholly ripe they have a very agreeable bitter-sweet flavour, but not so strong as that of the pineapple. They are succulent, fresh and easy to digest. They refresh one well during the hot weather; the skin, which is tender, is peeled off; all the rest is pulp. They grow in warm climates and need irrigation, Although because of their shape they are called *pepinos*, many of them are wholly round, and there are others of different shapes; so even in their figure they are not really like true cucumbers. This plant I do not remember having seen in New Spain [Mexico] nor on the islands [Caribbean], but only on the plains of Peru" (Acosta, 1940, 275–276; Acosta, 1954, 113).

Amongst the common fruits of the plains of Trujillo, Peru, Vázquez de Espinosa included the pepino, adding:

"['The Indian village of Mansiche is a quarter league from the city, with delicious vegetables and fruit, particularly Peruvian cucumbers; these are of many kinds and] varieties; those from this village [have the reputation all over the Kingdom of] being the best in Peru [since they are among the best and most delicious]. The plant resembles a pepper plant, but the leaf is smaller and more elaborate [in its color and the [—] of its shape] is like a tomato leaf. ['The cucumber] is [there are] of many sorts—purple [likewise there are] yellow and white (Marg.: and of other colors), and they are very smooth. They must be ripe when eaten for when green [they are worth nothing] they are no good; they come long, round and in [many] other shapes, small and large. They taste very good when fully ripe; they are very juicy and refreshing, and are good for the kidneys and digestion; you peel off the skin,

which is very soft and thin, and then eat it all. This fruit [I never saw in all of New Spain and Honduras, or in the islands; it] only grows in Peru." (Vázquez de Espinosa, 1942, 390, 393–394; Vázquez de Espinosa, 1948, 365, 367, 368).

Cobo described the pepino with praiseworthy exactness. He noted varieties which were murrey, yellow, striped white and others, but states that the commonest is murrey striped with bands of different color. "The best grew on the valleys along the coast of Peru; those from the valleys of Trujillo, Iça and Chincha are specially famous. They require hot and sandy soil; although they have been taken to New Spain [Mexico], they do not yield as well there as here, since the climate is not so favorable. At the Atrisco Valley, I saw them in the Carmen Convent; I tried them myself and found them tasteless, without the sweetness of those in this Kingdom. The juice, mixed with red ointment, is valuable for 'heat of the kidneys.' In the Quechua language it is called *Cachum* and in Aymara, *Cachuma*" (Cobo, 1891, II, 381–383; Cobo, 1956, I, 177). In another place, Cobo asserted that, while it grows very well in America, the Spanish cucumber (*Cucumis*) is used merely as a vegetable, whereas the native "cucumber" or pepino (*Solanum*) is preferred as an edible fruit (Cobo, 1891, II, 436–437; Cobo, 1956, I, 418).

Miguel Feyjoo, in his description of the Province of Trujillo, Peru, about the middle of the 18th Century, included the pepino amongst the cultivated native fruits (Feyjoo, 1763, 13).

Amongst the plants collected by the botanist Hipólito Ruíz in Lima and its vicinity and in the Andean valleys, in the first half of the year 1778, he listed pepino as *Solanum variegatum*. The fruits, he reported, were very commonly consumed in Peru, and he erroneously

attributed to them the characteristic of producing, if eaten in excess, tertian fevers and dysentery with tenesmus (Ruíz, 1952, I, 29). Describing the products of Lurín, near Lima, he mentioned again the "native cucumber." He wrote that this shrub blossoms profusely and that the fruits are usually yellowish, whitish or spotted with murrey, violet and red; he repeats the statement about the presumed tendency of the fruit to produce the diseases mentioned above, adding: "this plant is propagated by the stems, because by the seeds it takes two years to produce fruit, after having been transplanted from the nursery in which they were sown" (Ruíz, 1952, I, 53–54).

Latcham reported that *Solanum muricatum* is cultivated in the northern part of Chile; but he assumed that, because of the absence of an Araucanian name, the species had been introduced by the Incas (Latcham, 1936, 214–216).

BIBLIOGRAPHY

Acosta, Joseph de, 1940. Historia natural y moral de las Indias. . . Fondo de Cultura Económica, Mexico. lxxxv+638 pp.

——, 1954. Obras del P. . . , de la Compañía de Jesús. Estudio preliminar y edición del P. Francisco Mateos, de la misma Compañía. Biblioteca de Autores Españoles, Madrid. xlix+633 pp.

Altolaguirre y Duvale, Angel de, 1908. Relaciones geográficas de la gobernación de Venezuela (1767–68). Con prólogo y notas de. . . Publicaciones de la Real Sociedad Geográfica. Imp. del Patronato de Huérfanos de Admon. Militar. Madrid. li+350 pp.

Alvarado, Lisandro, 1953. Glosario de voces indígenas de Venezuela. Voces geográficas (Trabajo inédito complementario) Obras Completas, Vol. I. Tip. La Nación. Caracas. 422+(iii) pp.

André, Edouard, 1879. L'Amérique equinoxielle. Le Tour du Monde. Paris. (1879) 2nd sem. xxxviii.

Bertonio, Ludovico, 1612. Vocabvlario de la lengva aymara. Primera parte, donde por abecedario se ponen en primer lugar los Vocablos de la lengua española para buscar los que les corresponden en la lengua Aymara. Compuesto por el P. Ludovico Bertonia Italiano de la Compañía de Iesús en la prouincia del Pirú, de las Indias Occidentales, Natural de la Roca contrada de la Marca de Ancona. 474 pp. Segunda parte del vocabvlario en la qval por orden del ABC se ponen en primer lugar los vocablos de la lengua Aymara para hallar los que le corresponden en la Española. Juli. 399 pp.

Bukosov, S.M., 1930. The cultivated plants of Mexico, Guatemala and Colombia. With supplementary articles by N.N. Kulesov, N.E. Zhiteneva, V.I. Mazkievicz and C.M. Popova, with 307 photographs and maps. Composed on the basis of the data and materials of the Expedition of the Institute of Applied Botany in 1925–6. Leningrad. 553+16 (illustr.)+xxxvii+v pp., 3 lám.

Cárdenas, Martín, 1950. Plantas alimentícias nativas de los Andes de Bolivia. Folia Universitaria, Nos. 2, 3, 4. Cochabamba. 25 pp.

Cieza de León, Pedro, 1924. La crónica general del Perú. Anotada y concordada con las crónicas de Indias—por Horacio H. Urteaga. Vol. I. Lib. e. Imp. Gil. Col. Urteaga. Historiadores Clásicos del Perú. Lima. Vol. VII, xvi+346 pp.

——, 1880. Segunda parte de la Crónica del Perú, que trata del Señorío de los Incas Yupanquis y de sus grandes hechos y gobernación. Publícala Marcos Jiménez de la Espada. Biblioteca Ultramarina. Madrid. 20+279 pp.

Cobo, Bernabé, 1890–91. Historia del Nuevo Mundo. Por el P. . . de la Compañía de Jesús, publicada por primera vez con notas y otras ilustraciones de D. Marcos Jiménez de la Espada. Sociedad

de Bibliófilos Andaluces. Sevilla. 1890—Vol. I—viii+530 pp. 1891, Vol. II, 467 pp.

——, 1956. Obras del P. . . de la Compañía de Jesús—Estudio preliminar y edición del P. Francisco Mateos, de la misma Compañía. Biblioteca de Autores Españoles. Madrid. Gráficas Orbe. 1956, Vol. I, xlvii+439 pp.; Vol. II, 516 pp.

Domingo de Santo Tomás (Fr.), 1560. Lexicon, o vocabulario de la lengua general del Perv. . . Francisco Fernández de Córdova, Impresor de la M. R. Con Privilegio. viii+179 folios.

——, 1951. Id. Facsimile edition published, with a foreword, by Raúl Porras Barrenechea. Edición del Instituto de Historia. Lima. 374 pp.

Fejos, Paul, 1940. Report on the exploration of the region of the Rio Colorado, Departamento de Madre de Dios, by the Wenner-Gren Scientific Expedition to Hispanic America. 1940–42. Lima. Mimeogr. 31+6 pp.

Fennel, Joseph L., 1948. Cocona—a desirable new fruit. Foreign Agriculture. Washington, D.C., Vol. XII. August. No. 8; pp. 181–182.

Feyjoo (de Sosa), Miguel, 1763. Relación descriptiva de la ciudad, y provincia de Truxillo del Perú, con noticias exactas de su estado político. . . Imprenta del Real y Supremo Consejo de Indias. Madrid. xii+164 pp. y 3 planos.

Gattoni, Luis A., 1935. La industria del jugo de la naranjilla ecuatoriana. Hoja de Divulgación Agrícola. Ministerio de O. Públicas, Agricultura y Fomento. Dirección Gral. de Agric., Comercio e Industrias. Imprenta Nal. de Quito. 15 pp.

González Holguín, Diego, 1608. Vocavulario de la lengva general de todo el Perv llamada lengua Qquichua, o del Inca. Corregido y renovado conforme a la propiedad cortesana del Cuzco. Ciudad de los Reyes. 4+365+332 pp.

——, 1952. Id. New edition with foreword by Raúl Porras Barrenechea. . . Instituto de Historia. Impr. de Santa María. Lima. xliv +697 pp.

Gumilla, Joseph, 1741. El Orinoco ilustrado. Historia natural, civil y geográfica, de este gran río, y de sus caudalosas vertientes. . . Manuel Fernández. Madrid. 580+19 de índice pp.

——, 1944. El Orinoco ilustrado. Historia natural, civil y geográfica de este gran río. Biblioteca Popular de Cultura Colombiana. Bogotá. Vol. I. 1944. 360 pp.; Vol. II. 1944. 334 pp.

——, 1955. Id. . . . Biblioteca de la Presidencia de Colombia. No. 8. Editorial ABC. Bogotá. 427 pp.

Humboldt, Alejandro de, 1942. Viaje a las regiones equinocciales del Nuevo Continente—hecho en 1799–1800–1801, 1802, 1803 y 1804 por. . . y A. Bonpland. Biblioteca Venezolana de Cultura. Trans-

lated by Lisandro Alvarado and others. Caracas. Vol. IV. 606 pp.
Jijón y Caamaño, Jacinto, 1940–41. El Ecuador interandino y occidental antes de la Conquista Castellana. Edit. Ecuatoriana. Quito. Vol. I. 1940. 556 pp.; Vol. II. 1941. 555 pp.
Jiménez de la Espada. Marcos, 1897. Relaciones geográficas de Indias. Peru. Ministerio de Fomento. Madrid. Vol. III. xl+276+clxxv pp.
Juan de Santa Gertrudis Serra (Fr.), 1956. Maravillas de la naturaleza. T.I. Primera y segunda parte. Bogotá. (Biblioteca Presidencia de la República.) Vol. 28. 423 pp.
Karsten, Rafael, 1935. The head-hunters of western Amazons. The life and culture of the Jibaro Indians of eastern Ecuador and Peru. Helsingfors. 598 pp.
Latcham, Ricardo E(duardo), 1936. La agricultura precolombina en Chile y los países vecinos. Edic. Universidad de Chile. Santiago. viii+336 pp.
Lira, Jorge A, 1945. Diccionario Kkechuwa-Espanol (Universidad Nacional de Tucumán—Departamento de Linguística y Folk-lore). xii. Talleres Gráficos Miguel Violetto. Tucumán. 1200 pp.
Magnin, Juan, 1940. Breve descripción de la Provincia de Quito y de sus misiones de Succumbios de religiosos de S. Franco., de Maynas de Pp. de la Compa. de Jhs. a las orillas del gran Río Maranon, hecha para el Mapa que se hizo el ano 1740, por el P. . . , de dha. Compa., missionero en dichas Missiones. Revista de Indias. Ano I, No. 1. Instituto Gonzálo Fernández de Oviedo. Madrid. pp. 151–185.
Michelena y Rojas, F., 1867. Exploración oficial por la primera vez desde el norte de la América del Sur. . . En los años de 1855 hasta 1859, por. . . A. Lacroix. Verboeckhoven & Co. Bruselas. 684 pp.
Patiño, Victor Manuel, 1958. El cachipay o pijibay (*Guilielma Gasipaes* (HBK.) Bailey) y su papel en la cultura y en la economía de los pueblos indígenas de America intertropical. América Indígena. Mexico. Vol. XVIII. No. 3, pp. 177–204: No. 4, pp. 299–332.
Ramos Pérez, Demetrio, 1946. El tratado de límites de 1750 y la expedición de Iturriaga al Orinoco. Prol. de Armando Melón y Ruíz de Gordejuela. Cons. Sup. de Invest. Científ. Inst. Juan Sebastián de Elcano. Gráficas Versal. Madrid. 537 pp.
Ruíz, Hipólito, 1952. Relación histórica del viage, que hizo a los Reynos del Perú y Chile el botánico don. . . en el año de 1777 hasta el año de 1788, en cuya época regresó a Madrid. . . Ed. Dr. Jaime Jaramillo-Arango. Real Academia de Ciencias Exactas, Físicas y Naturales de Madrid. Talleres Gráficos de Cándido Bermejo. Madrid. Vol. I (Texto): xliv+526 pp.
Sarmiento, Alberto, 1958. Monografía científica del oriente ecuatoriano. Quito. 318 pp.

Schultes, Richard Evans, 1949. Plantae Colombianae XII. De plantis principaliter Amazoniae Colombianae Investigationes. Botanical Museum Leaflets, Harvard Univ. Vol. 14, No. 2, pp. 21–47 and plate X.

——, 1958. A little known cultivated plant from northern South America. Botanical Museum Leaflets, Harvard Univ. Vol. 18, No. 5, pp. 229–244 and plates XLVI to XLIX.

—— and Cuatrecasas, José, 1953. Notes on the cultivated lulo. Botanical Museum Leaflets, Harvard Univ. Vol. 16, No. 5, pp. 97–105.

Serra, Juan de Santa Gertrudis (See *Juan de Santa Gertrudis*).

Tascón, Leonardo, 1934? Quechuismos usados en Colombia. Ed. T. E. Tascón and Jorge H. Tascón. Bogotá. 153 pp.

Tavera Acosta, Bartolomé, 1954. Rionegro; reseña etnográfica, histórica y geográfica del Territorio Amazonas. Ed. 3, Caracas. 309 pp., illustr.

Toscano Mateus, Humberto, 1953. El espanol en el Ecuador. Madrid. 478 pp.

Vázquez de Espinosa, Antonio, 1942. Compendium and description of the West Indies. Translated by Charles Upson Clark. Smithsonian Institution. Vol. 102, Publ. 3646, Washington, D.C. xii+862 pp.

——, 1948. Compendio y descripción de las Indias Occidentales. Transcrito del manuscrito original por Charles Upson Clark. Smithsonian Miscellaneous Collections. Vol. 108, Washington, D.C. xii +801 pp.

Velasco, Juan de, 1927. Historia del Reino de Quito en la América meridional—escrita por el Pbro. Don. . . —nativo del mismo reino. Vol I and part 1. 1789. Imprenta Nacional, Quito. 270+iv pp.

Villaquirán, Vicente, 1939. Historia y Antigüedades. Boletín de Historia y Antigüedades. Cali. 61–66: pp. 204–220.

Villavicencio, Manuel, 1858. Geografía de la República del Ecuador. New York. Imprenta de Robert Craighead. 505 pp., 2 maps and plates.

Wolf, Teodoro, 1892. Geografía y geología del Ecuador. Published by order of the Supreme Government of the Republic. With 12 plates, 47 text figures and 2 maps. Leipzig. Tip. de F. A. Brockhaus. xii+671 pp.

Zamora, Alonso de, 1701. Historia de la Prouincia de San Antonino del Nuevo Reyno de Granada, del orden de predicadores. . . Barcelona. Imprenta de Joseph de Llopis. (xx)+537+(xx) pp.

——, 1930. Historia de la Provincia de San Antonino del Nuevo Reino de Granada. Prólogo de Caracciolo Parra y notas ilustrativas del mismo y de Fr. Andrés Mesanza. Parra León Hermanos. Caracas. 559 pp. Folio.

EDIBLE FRUITS OF SOLANUM IN COLOMBIA

BY
RICHARD EVANS SCHULTES
AND
RAFAEL ROMERO-CASTAÑEDA[1]

ONE of the largest and most interesting plant families in tropical South America is the Solanaceae. The world has acquired from this continent a number of solanaceous economic plants of outstanding value, such as *Lycopersicon esculentum* Mill. (tomato): *Cyphomandra betacea* (Cav.) Sendt. (tree tomato): *Nicotiana Tabacum* L. (tobacco): *Solanum tuberosum* L. (potato): and sundry narcotics. There are, however, other species of lesser economic importance, grown locally, which have never been extensively adopted by peoples in other regions. This family, especially as it is represented in the Andes, merits much closer taxonomic and agronomic investigation. It is well within the realm of probability that new food or drug plants will be found when such a concerted study is pursued.

The genus Solanum contains some of the most poisonous members of the family, yet a few of the species yield edible berries which are utilized by the local inhabitants as fruits or as the source of refreshing and probably

[1] Instituto de Ciencias Naturales, Bogotá, Colombia. The illustrations reproduced in this paper have been made possible through a grant from the National Science Foundation.

vitamine-rich beverages. Our information on these edible species of Solanum is sparse, and, in some cases, its reliability is suspect. This is due primarily to the difficulty of precise identification of collections of Solanum, one of the largest genera of plants and one which, like many others in the family, suffers woefully from lack of modern taxonomic revision. There are undoubtedly an appreciable number of new species in the genus, in spite of the many concepts already described, and it appears that perhaps some of the species locally cultivated as economic plants fall into this category.

The present paper is offered as a preliminary summary of our knowledge of Colombian species of Solanum cultivated for their edible fruits. Much of the information contained in this summary has resulted from the field investigations of the authors and their botanical colleagues. It continues partial studies by both of the authors in previous articles and in a book: Schultes, R. E. and J. Cuatrecasas: "Notes on the cultivated lulo" in Bot. Mus. Leafl., Harvard Univ. 16 (1953) 97; Schultes, R. E.: "A little known cultivated plant from northern South America" ibid. 18 (1958) 229; and Romero-Castañeda, R.: "Frutas silvestres de Colombia" 1 (1961) 282–292. We have not felt constrained to include literature references to Solanum species with edible fruit without seeing voucher specimens ourselves. There remains open, obviously, an extensive field for future studies of this subject along both academic and practical lines of research. We hope that this brief contribution may stimulate studies of such a nature.

Solanum alibile *R. E. Schultes sp. nov.*

Frutex usque ad quattuor ped. altus, robustior, subscandens. Rami robusti, teretes, lepidoto-pubescentes, cortice brunneo. Ramuli densissime albo-stellato-tomen-

tosi. Folia grossiuscule membranacea, circiter ovata vel irregulariter elliptica, usque ad 50 cm. longa, 38–40 cm. lata (probabiliter majora), basi inaequaliter truncata, apice abrupte acuminata vel subacuta, margine distantissime et profundissime sinuata, valde petiolata (petiolis usque ad 9 cm. longis, densissime albo-stellato-tomentosis), supra dense albido-sericea, infra regulariter albido-stellata; venis omnino stellatis. Inflorescentiae cymosae, laterales, breviter pedunculatae, pauciflorae. Flores pedicellati usque ad 1 cm. longi, 3 mm. in diametro, densissime molliterque stellato-pilosi. Calycis lobi aliquid crassulentes, triangulari-ovati, acuti, usque ad 12 mm. longi, extus maxime densissime molliterque albido-stellati, intus subglabri sed minute lepidote, fructu persistentes. Corolla valde membranacea, lobis albido-viridibus, oblongis, usque ad 18 mm. longis, 6 mm. latis, intus subglabris, extus dense stellato-pilosis. Anthera flava, erecta, plusminusve 8 mm. longa. Stylus teres, 5 mm. longus. Ovarium globosum, dense albido-sericeum, 2.5 mm. in diametro. Fructus globosus vel subglobosus, 9–9.5 cm. in diametro, maturitate rufescens, dense minuteque stellato-tomentulosus: indumento faciliter caduco, maturitate subglabrescens. Pulpa acidulosa. Semina numerosissima, compressa, in circuiter ovalia, 2–3 mm. longa, plusminusve 1.8–2 mm. lata, straminea.

COLOMBIA: Comisaría del Putumayo, Río Putumayo, Puerto Asís, altitude about 200 m. "Fruit orange-red. Size of very large orange, covered with caducous hairs. Leaves and petioles spineless. Shrub 3–4 feet tall. Cultivated. *Lulo.*" August 2, 1960, *Richard Evans Schultes 22571* (TYPE in Econ. Herb. Oakes Ames; DUPLICATE TYPE in Herb. Nac. Col.).

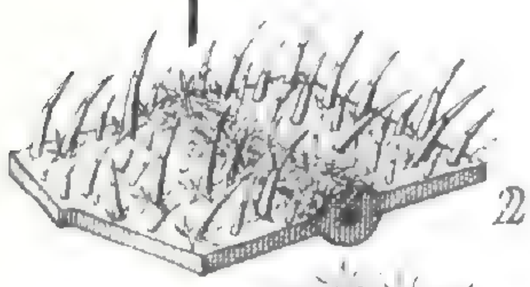
Solanum alibile, so named because of its extensive local use as a fruit and source of a refreshing beverage, is closely related to *S. Topiro*. More extensive field or monographic work might indicate that it should be accorded only varietal rank. The inhabitants readily distinguish

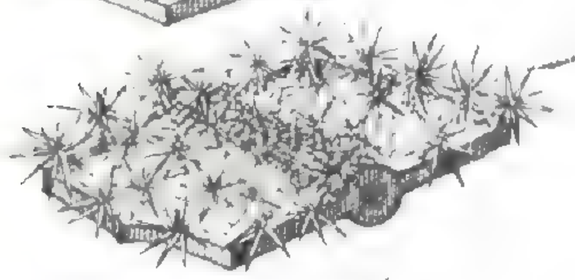
EXPLANATION OF THE ILLUSTRATION

PLATE XXXII. SOLANUM ALIBILE *R. E. Schultes*. 1, leaf, approximately one half natural size. 2, portion of upper surface of leaf, greatly enlarged. 3, portion of nether surface of leaf, greatly enlarged. 4, young leaves and buds, approximately one half natural size. 5, fruit, one half natural size. 6, flower, approximately one half natural size.

Drawn by ELMER W. SMITH

SOLANUM alibile R.E.Schultes


2


3

6

4

5

1

E.R.Schultes

the two, however, and state that the fruits of *Solanum alibile* are less acidulous than are those of *S. Topiro*.

The fruit of *Solanum alibile* is normally perfectly globose (instead of being ovoid) and more than twice as large (9–9.5 cm. instead of 4.5 cm. in diameter) than those of *S. Topiro*. There are, likewise, significant differences in the form and coloration of the indument of the leaves and floral segments.

Solanum alibile and its fruits are called *lulo* by the inhabitants of the Comisaría del Putumayo, most of whom are recent settlers from the more populous parts of Colombia where, in the highland areas, this vernacular name applies to *S. quitoense*.

Solanum georgicum *R. E. Schultes sp. nov.*

Frutex usque ad quattuor ped. altus, robustior, erectus. Rami robusti, teretes, dense albido-stellati, cortice griselli, partibus omnibus spinis armati. Ramuli similes. Folia grossiuscule membranacea, circuiter ovata vel irregulariter lateque elliptica, lamina usque ad 35 cm. longa, 28 cm. lata, basi inaequaliter truncata, apice abrupte acuminata vel subacuta, margine distante profundeque sinuata, valde petiolata (petiolis usque ad 5 cm. longis, maxime densissime albido-stellatis), supra dense regulariterque albido-sericea, infra dense albido-stellata (statu juvenile aureo-sericea), venis utroque latere stellatis et spinis stramineis sed basi fuscis, usque ad 15 mm. conspicue armatis. Inflorescentiae cymosae, laterales, breviter pedunculatae, pauciflorae. Flores pedicellati; pedicelli usque ad 6–7 mm. longi, dense stellati. Calycis lobi aliquid crassulentes, triangulari-ovati, valde acuti, leviter marginati, usque ad 10 mm. longi, extus densissime molliterque albido-stellati, intus dense albido-lepidoto; fructu persistentes. Corolla valde membranacea; lobis albido-viridibus, oblongis, subacutis, usque ad

12 mm. longis, 5–7 mm. latis, intus glabris, extus dense stellato-pilosis. Anthera flava, erecta, plusminusve 9 mm. longa. Stylus teres, 4–5 mm. longus. Ovarium globosum, dense et longe albido-sericeum, 2.5–3 mm. in diametro. Fructus perfecte globosus, plerumque 4.5 cm. in diametro, maturitate rufescens, dense minuteque tomentulosus, indumento faciliter caduco, maturitate subglabrescens. Pulpa aliquid acidulosa. Semina numerosissima, compressa, in circuiter ovalia, plusminusve 2.5 mm. longa, 2 mm. lata, straminea.

COLOMBIA: Comisaría del Putumayo, between Pepino and Mocoa, altitude about 700 m. "Cultivated. Flowers greenish white. Leaves very spiny. Height 2–4 ft. Fruit globose, ripening dark red, covered with caducous hairs. *Naranjilla.*" July 28, 1960, *Richard Evans Schultes 22554* (TYPE in Econ. Herb. Oakes Ames; DUPLICATE TYPE in Herb. Nac. Col.).—Comisaría del Putumayo, Río Putumayo, Puerto Asís, altitude about 200 m. "Shrub 2–3 feet tall. Fruit orange-red, small. Leaves spiny." August 2, 1960, *R. E. Schultes 22573.*

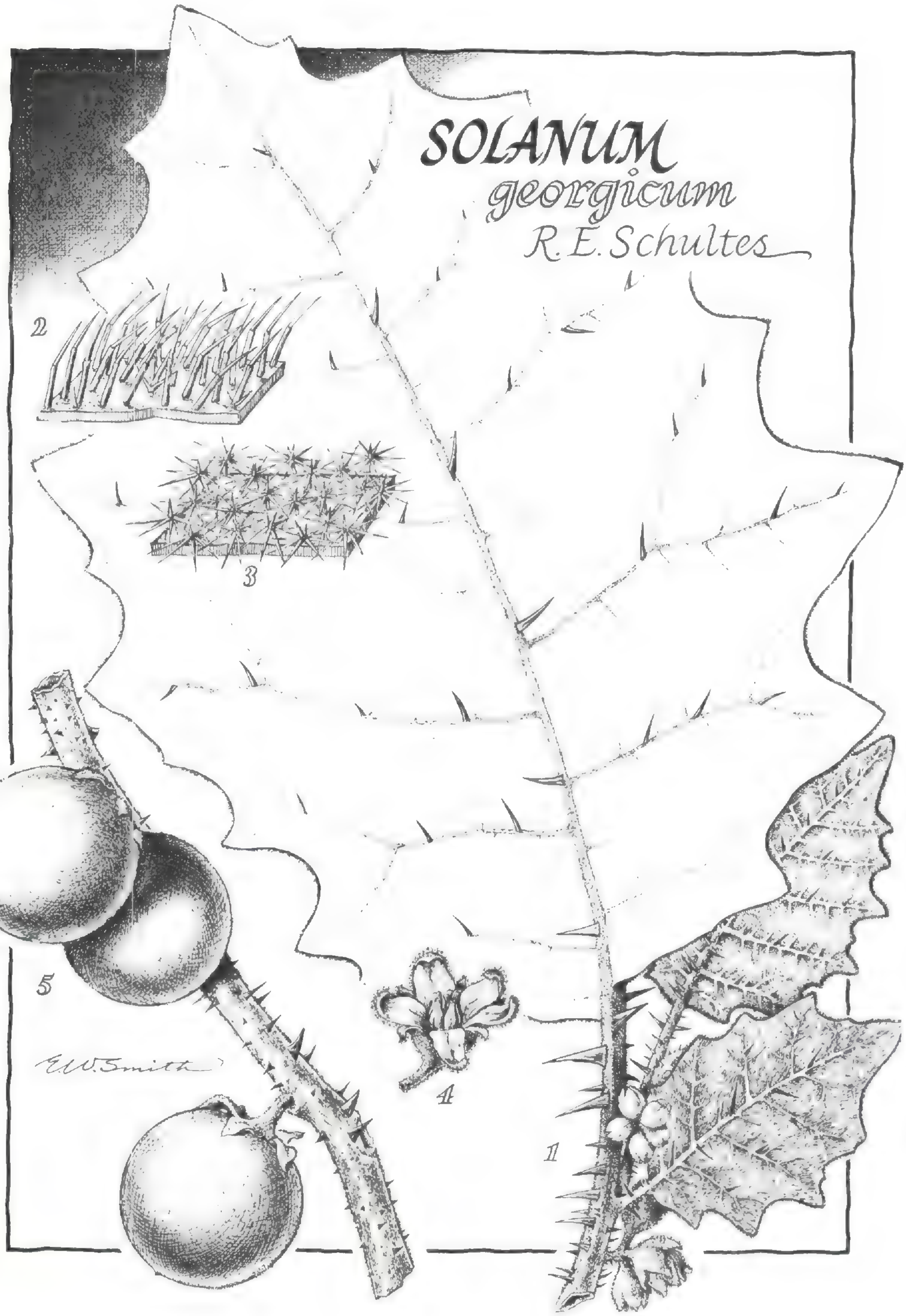
This new species is allied to *Solanum Topiro*, but it is distinguished by the inhabitants of the region who apply different common names to the two plants. *Solanum Topiro*, which is not found in the Comisaría del Putumayo as high as 700 meters, is called *cocona*, whereas *S. georgicum* is known as *naranjilla*, the term which, in the southern Colombian Andes, refers to *S. quitoense*. The inhabitants of the Putumayo are quick to point out two other important differences: *S. georgicum* is conspicuously spiny on the stems and along the nerves of the leaves and has perfectly globose fruits, whereas *S. Topiro* is unarmed and usually has ovoid fruits.

The berry of *Solanum georgicum* is eaten directly as a fruit and is employed in the preparation of a refreshing, acidulous beverage. The plant is cultivated, but in a haphazard way, growing up along roadsides and on the edge of agricultural plots (whence its specific epithet) without special care. It appears to be a wild species which has

EXPLANATION OF THE ILLUSTRATION

PLATE XXXIII. SOLANUM GEORGICUM *R. E. Schultes.* 1, leaves and buds, approximately one half natural size. 2, portion of upper surface of leaf, greatly enlarged. 3, portion of nether surface of leaf, greatly enlarged. 4, flower, approximately one half natural size. 5, fruiting branch, approximately one half natural size.

Drawn by ELMER W. SMITH


SOLANUM
georgicum
R.E. Schultes
2
3
5
E.W. Smith
4
1

EXPLANATION OF THE ILLUSTRATION

PLATE XXXIV. SOLANUM GEORGICUM *R. E. Schultes.*
Photograph of a flowering branch of the type plant.
Photograph by RICHARD EVANS SCHULTES

Plate XXXIV

EXPLANATION OF THE ILLUSTRATION

PLATE XXXV. SOLANUM GEORGICUM *R. E. Schultes.*
Photograph of a fruiting branch of the type plant.
Photograph by RICHARD EVANS SCHULTES

Plate XXXV

become but recently only partly domesticated. It is said by the natives, however, never to be found in the wild away from man's influence.

Solanum liximitante *R. E. Schultes sp. nov.*

Frutex usque ad plusminusve quattuor ped. altus. Truncus ramique robustiores, basi spinosi. Ramuli usualiter sine spinis, glabri, cinereo-virides. Ramuli terminales puberulentes, cinereo-fusci. Folia membranacea, atroviridia, supra conspicue bullata, subtus cinereo-violacea (vivo), in circuiter ovata, maturitate plusminusve 27 cm. longa, 20–22 cm. lata, basi cuneata ad subtruncata, apice acuta, margine profundissime sinuata, valde petiolata (petiolus usque ad 6–7 cm. longus, dense cinereo-pubescens; supra remotissime stellato-pubescentes sed nervum centralium versus densissime stellato-pubescentes, minutissime scrobiculata; subtus molliter et dense stellata; nervis utroque latere conspicuis. Inflorescentiae cymosae, laterales, breviter pedunculatae, pauciflorae. Flores pedicellati; pedicellis usque ad 3 mm. longi, dense albido-stellato-pubescentes. Calyx cymbiformis, aliquid coriaceus, inconspicue 5-dentatus, usque ad 4 mm. longus, intus glaber, extus dense flavo- vel albido-stellatus. Corolla subcarnosa, albido-violacea (vivo), lobis oblongo-ovatis, usque ad plusminusve 6 mm. longis, apice rotundatis cucullatisque, margine valde reflexis, intus glabris, extus dense stellato-pubescentibus. Antherae erectae, flavae, lineares, quam corolla longae. Stylus plusminusve clavatus, usque ad 3 mm. longus. Ovarium dense stellatum. Fructus globosus, usque ad 1.5 cm. in diametro, maturitate sanguineus, dense et minutissime stellatus sed maturitate subglabrescens. Semina numerosa, plana, in circuiter ovalia, 2 mm. longa.

Colombia: Comisaria del Vaupés, Rio Vaupés, Mitú, at mouth of Río Kuduyarí. "Fruit red. Flowers whitish violet. Leaves purplish

beneath, dark green above, crinkled. Plant with spines on thick, basal stem, glabrous on younger growth. Cultivated." August 12, 1960, *Richard Evans Schultes 22583* (TYPE in Econ. Herb. Oakes Ames).—Same locality. "*Lulo.* Flores amarillo-verdosas. Fruto esférico, amarillento, comestible. Yerba cultivada." June 22–30, 1958, *H. García-Barriga, R. E. Schultes & H. Blohm 15771a.*—Comisaría del Vaupés, Río Inirída, vicinity of Santa Rosa. Alt. 220 m. "Hierba. Frutos rojos." January 25, 1953, *A. Fernandez 1961.*

Solanum liximitante appears to be related to *S. straminifolium*, but it has a very different appearance because of its conspicuously bullate leaves. *Solanum straminifolium* bears strong spines usually on all parts of the stem, branches and on the ultimate twigs as well as along the midrib and secondary veins of the leaves, whereas in *S. liximitante* the leaves and twigs, and often the branches themselves, are unarmed. There are, furthermore, certain interesting floral characters in *Solanum liximitante*, such as the very strongly cucullate corolla lobes with inrolled margins, which are not matched in *S. straminifolium*. The fruit of *Solanum liximitante* is usually somewhat smaller than that of *S. straminifolium*.

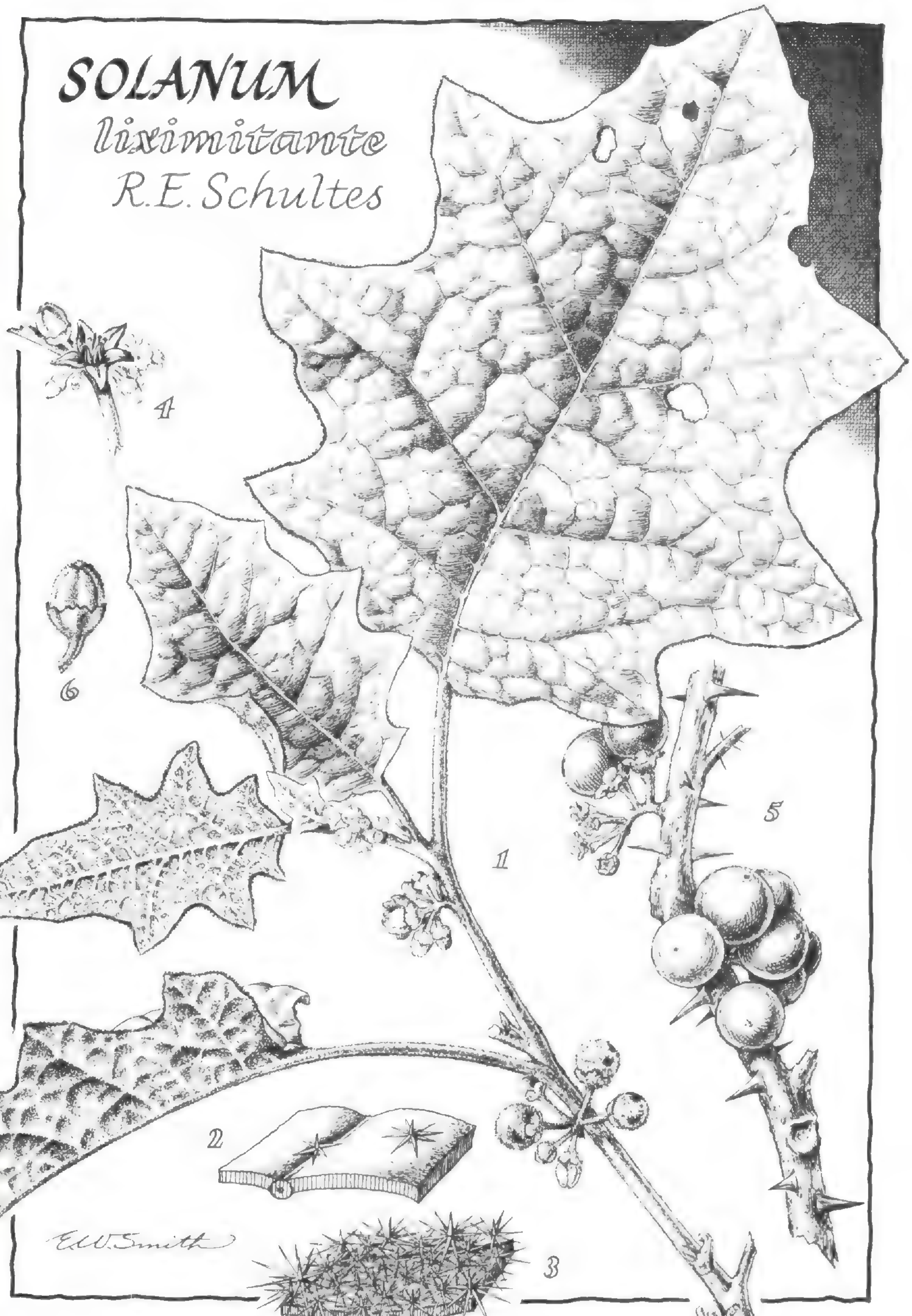
The specific epithet of *Solanum liximitante* means "resembling a sutler or camp-flower" and has been chosen to emphasize the semi-domesticated state in which this species finds itself. It grows with no care near and in cultivated Indian plots. Footpaths through the growths of Manihot and Erythroxylon are often thickly populated by bushes of *Solanum liximitante* which have come up from seeds casually spread when pieces of the fruit have been spit out by Indians at work in the fields.

In the Amazonas and Vaupés of Colombia, *Solanum liximitante* is known by the following Indian names: Karijona (Río Caquetá)—*chĕ-hore-kĕ-noo-roo;* Maku (Río Piraparaná)—*beñ;* Makuna (Río Apaporis)—*ĕ-tó;* Miraña (Río Caquetá)—*kö-mö-hĕ-ro-ya* (*kö-mö-hĕ* = "water turtle"): Puinave (living on Río Apaporis)—*pee-pee-ká;*

EXPLANATION OF THE ILLUSTRATION

PLATE XXXVI. SOLANUM LIXIMITANTE *R. E. Schultes.* 1, branch, approximately one half natural size. 2, portion of upper surface of leaf, greatly enlarged. 3, portion of nether surface of leaf, greatly enlarged. 4, flower and buds, approximately one half natural size. 5, portion of stem with fruits, approximately one half natural size. 6, bud, approximately one and one half times natural size.

Drawn by ELMER W. SMITH


SOLANUM
liximitante
R.E. Schultes
4
6
1
5
2
3
E.C.V. Smith

EXPLANATION OF THE ILLUSTRATION

PLATE XXXVII. SOLANUM LIXIMITANTE *R. E. Schultes*.
Photograph of fruiting branches of the type plant.
Photograph by RICHARD EVANS SCHULTES

Plate XXXVII

Tanimuka (Río Popeyacá)—*a-meé-má-ra*; Yukuna (Río Miritiparaná)—*loo-poo-po-ró-la* (*loo-poo* = "cayman"). Karapana (Río Kananarí)—*lĕ-tó-ma-ta*.

Solanum muricatum *Aiton* Hort. Kew., ed. 1, 1 (1789) 250.

Subshrub unarmed, up to 2–3 feet tall. Branches terete, greyish green in life, often verrucose-scabrid. Twigs reddish brown, very sparsely beset with simple, soft white hairs. Leaves membranaceous, oblong-lanceolate, marginally entire or slightly undulate (rarely ternate), apex acuminate, basally usually somewhat cuneate, strongly petiolate (petiole usually 3–6 cm. long, more or less marginate); upper surface white-sericeous (hairs single, but each comprising a main shaft with a minute, articulated tip); nether surface minutely white-squamate, sericeous (as upper surface); veins subconspicuous; midrib very conspicuous beneath. Inflorescence lateral, lax, few-flowered cymes. Flowers about 2 cm. in diameter, pedicellate; pedicels up to about 5 mm. long, sparsely white-sericeous. Calyx lobes triangular, apically attenuate, up to 12.5 mm. long, densely sericeous without, subglabrous within. Corolla thinly membranaceous, bright blue, deeply lobed, lobes ovate, apically acute, about 20 mm. long, pubescent without, glabrous within. Anthers yellow, erect, 6–7 mm. long. Style filiform, up to 9 mm. long. Ovary ovoid. Fruit very variable under cultivation; usually ovoid or elongate-ovoid, long-pedunculate, drooping, smooth, whitish or yellow, sometimes yellow-green, usually with purplish or reddish purple spots or lines, 5–20 cm. long. Pulp yellow with cucumber-like flavor. Seeds usually lacking in cultivated material.

COLOMBIA: Departamento de Caldas (?), "Quindío" (?) 1856, *J. Triana 3855/6*.—Departamento del Cauca, El Tambo, Cordillera Occidental, vertiente oriental, altitude about 1700 m. *K. von Sneidern 4817*.—Departamento de Cundinamarca, Bogotá, altitude 2600 m. "Nom-

bres vulgares: *pepino redondo*, *pepino morado*. Cultivado." November 1856, *J. Triana 3855/65*. Bogotá, Chapinero. "Nombre vulgare: *pepino morado*. Cultivado." *E. Perez-Arbeláez 2507*.—Departamento del Huila, Parque Arqueológico de Sán Agustín, altitude about 1700 m. "Nombre vulgar: *pepino*. Corolla blanca." *R. Romero-Castañeda 6709*.—Comisaría del Putumayo, road from Sachamates to Mocoa, above road camp "El Pepino," altitude about 4200 feet. "Cultivated. Common name: *pepino*." December 9, 1941, *R. E. Schultes & C. E. Smith 3046*.

Solanum muricatum, known from the Andean regions from Chile north to Colombia, has been cultivated since pre-Columbian times in the temperate highlands between 4200 and 7500 feet. A domesticated plant, it is represented now by several distinct cultivated forms, differing primarily in the fruit. (Popenoe, W.: "Economic fruit-bearing plants of Ecuador" in Contrib. U.S. Nat. Herb. 24 (1924) 133; U.S. Dept. Agric. Bur. Pl. Ind.: "Inventory of seeds and plants imported by the Office of Foreign Seed and Plant Introduction during the period from Jan. 1 to March 31, 1917" (Jan. 30, 1922) 17.) It is most commonly known as *pepino* ("cucumber") but it has other names, such as *pepo* in Lima, in reference to the shape of the fruit. In Colombia, it is referred to usually as *pepino morado* or *pepino redondo*.

Solanum muricatum, although described by Aiton as native to Chile and Peru, is native probably to Ecuador (where it appears to be most variable today) and was spread southward through human activity. In Colombia, its range is restricted essentially to the southern parts of the country, although it may occasionally be cultivated in the north (Perez-Arbeláez, E.: "Plantas útiles de Colombia," ed. 3 (1956) 709). It now occurs in Middle America, where it has doubtlessly been distributed in relatively recent times (Standley, P. C.: in Ann. Rept. Smithson. Inst. 1922 (1922) 317). It is an erect, usually spineless shrubby herb up to 2 or 3 feet in

height, with dense clusters of blue flowers somewhat less than an inch in diameter. The leaves are sometimes entire, but usually slightly undulate, occasionally trifoliate, linear-lanceolate to ovate, soft-pubescent. The fruit, an almost globose to ovoid or even elongate berry, measures usually 7 to 16 (sometimes 5 to 20) cm. in length. Most forms of the plant bear greenish, yellow or whitish fruits marked with purplish or reddish streaks or spots, but some may be basically pure yellow or pale green. It is juicy, aromatic and scented and somewhat acid, described frequently as resembling in taste "an acid eggplant." Most cultivated forms are said to produce seedless fruits. The plant is stated to yield fruit for three years, a crop every three or four months, and to begin to produce about five months after planting.

Too little is known about *Solanum muricatum*. The variability in fruit and the fact that some sources state that the plant may have spines might indicate that either more than one species or one or more definite botanical varieties are involved. Herbarium material is very scarce. A taxonomic study of variability in *pepino* over its whole range is long overdue.

This species was discussed as early as 1714 by Feuillée (in Journ. Obs. Phys. Math. Bot. (1714) 735, t. 26), who called it *Melongena laurifolia*, described it at length and published an illustration of it in his account of travels in Peru. It was first introduced to Europe apparently by the French horticulturist Thouin in 1785 (Aiton: loc. cit.) and, shortly thereafter, in 1789, described and given the name *Solanum muricatum* by Aiton at the Royal Botanical Gardens, Kew. The third botanical consideration of *pepino* was that of Ruíz and Pavón, the Spanish plant-explorers of Peru and Chile, who, in 1799, gave a full description of it, calling it *Solanum variegatum* and publishing an excellent drawing of the plant (Fl. Peruv. 2 (1799) 32, t. 162a).

There seems to have been no further horticultural interest in the species until 1882, when it was introduced into the United States by Eisen. (Anonymous: "Sundry investigations made during the year" in Bull. 37, Agr. Exper. Sta. Cornell Univ. (1891) 389–394; Bailey, L. H.: "Standard cyclopedia of horticulture" 3 (1930) 3182.) Because *pepino* means cucumber, Eisen thought it advisable to give the new introduction a more appropriate English common name. In this connection, he wrote (in Gard. Monthly 29 (1887) 84): "I suggested the name *melon shrub*, but through the error or the wisdom of a printer, the name was changed to *melon pear*, which I confess is not very appropriate. . . ." This name has persisted, however, in the American literature and, when the taste of the fruit—somewhat suggesting an acid musk melon—is taken into consideration, it is not altogether inappropriate. There was some success in cultivating *Solanum muricatum* in California and Florida (Anonymous, loc. cit.: in Am. Gard. 9 (1888) 265; Orch. and Gard. 10 (1888) 61), but in more northern states there was difficulty in its setting fruit. It does not do so well at low altitudes in Hawaii (Neal, M. C.: "In gardens of Hawaii" in Spec. Publ. Bishop Mus. 40 (1948) 657). At the turn of the century, Fairchild found that it had become very popular in the Canary Islands but that it was "doubtful whether it has found its proper niche there, where it can produce as delicate-flavored fruit as it does in the terraced gardens of Grand Canary."

In a very interesting and complete review of the culture and history of *pepino*, issued in 1891, the following recommendations were set forth: "The pepino is an unusually interesting plant, and if it could be made to set fruit more freely in the north, it would be an acquisition for the kitchen garden and for markets. It is a good ornamental plant. Altogether, it is deserving of a wider repu-

EXPLANATION OF THE ILLUSTRATION

PLATE XXXVIII. SOLANUM MURICATUM *Aiton* as illustrated by Fueillée in Journ. Obs. Phys. Math. Bot. (1714) t. 26 as *Melongena laurifolia*.

Plate XXXVIII

EXPLANATION OF THE ILLUSTRATION

PLATE XXXIX. SOLANUM MURICATUM *Aiton* (figure *a*) as illustrated by Ruiz and Pavón in Fl. Peruv. 2 (1799) t. 162 under the name *Solanum variegatum*.

Plate XXXIX

a SOLANUM *variegatum*. *b* SOLANUM *acutifolium*

EXPLANATION OF THE ILLUSTRATION

PLATE XL. SOLANUM MURICATUM *Aiton*. 1, branch, approximately one half natural size. 2, portion of upper surface of leaf, greatly enlarged. 3, flower, approximately one and one half times natural size.

Drawn by ELMER W. SMITH

PLATE XL

EXPLANATION OF THE ILLUSTRATION

PLATE XLI. Fruits of SOLANUM MURICATUM *Aiton*, showing variation in shape in plants grown near Las Palmas, Canary Islands. Negative No. 9790, United States Department of Agriculture, Bureau of Plant Industry.

Photograph by DAVID FAIRCHILD (April 1903)

Plate XLI

tation." Apparently, however, *Solanum muricatum* has never become more than a rare novelty in the United States, but the fruits do occasionally get into the markets locally in San Francisco and other parts of southern California.

Solanum platyphyllum *Humboldt & Bonpland ex Dunal* Sol. gen. aff. syn. (1816) 38.

Shrub occasionally weakly armed, rank, up to about 4 feet tall. Branches stout, terete. Twigs white-stellate-pubescent. Leaves membranaceous, ovate in outline, at maturity up to about 30 cm. long, 22 cm. wide, basally truncate, apically abruptly acute, marginally distantly, regularly and deeply minute, strongly petiolate (petiole up to about 10 cm. long, somewhat sulcate, brownish-stellate-pubescent); upper surface dark green, asperous-lepidote and very sparsely stellate-pubescent; nether surface pale green, densely and softly stellate-pilose; veins conspicuous especially beneath. Inflorescence a lateral, very short-peduncled, few-flowered cyme. Flowers pedicellate; pedicels more or less 5 mm. long, stellate-pilose. Calyx cup-shaped, crassulent, densely white-stellate-pilose without, white-lepidote within, apically sinuate, 5-dentate, more or less 3.5 mm. long. Corolla somewhat crassulent, lobes triangular, apically acute, marginally conspicuously inrolled, up to about 9 mm. long, very densely white-stellate-pubescent. Anthers yellow, erect, linear, about 7 mm. long. Style filiform, apically slightly clavate, 5.5 mm. long. Fruit globose, up to about 2 cm. in diameter, ripening purplish red, glabrous (only in young form with dense stellate hairs). Pulp strongly acid. Seeds numerous, flat, oval in outline, yellowish.

COLOMBIA: Comisaria del Amazonas, Trapécio amazónico, Loretoyacu River, altitude about 100 m. "Flowers white. Fruit edible." October 20–30, 1945, *R. E. Schultes 6642*.

Solanum platyphyllum is rather frequently found along the edge of cultivated plots and secondary growth in the Leticia area of the Colombian Amazonas. Like most other species of Solanum with edible fruits known from the Amazonian area, this species is not purposefully cultivated but springs up in abandoned sites from seeds which are cast away with uneaten portions of the fruit. The whitish fruits are rather sweet and are sought after for food by the Tikuna Indians of the region.

Little is known about *Solanum platyphyllum* as an economic plant. A collection (*Krukoff 9121*) from São Paulo de Olivença, a Brazilian town on the Amazon (Solimões) River slightly below Leticia, bears the notation: "Planted by Indians." Since the Indians of this area are likewise Tikunas, it may be that the plant is used only by this tribe. The species probably occurs also in Peruvian territory upstream from Leticia, but we have no information concerning its existence and use there.

Solanum quitoense *Lamarck* Illustr. 2 (1797) 16.

Solanum angulatum Ruíz & Pavón Fl. Peruv. 2 (1799) 36, t. 170, fig. a.

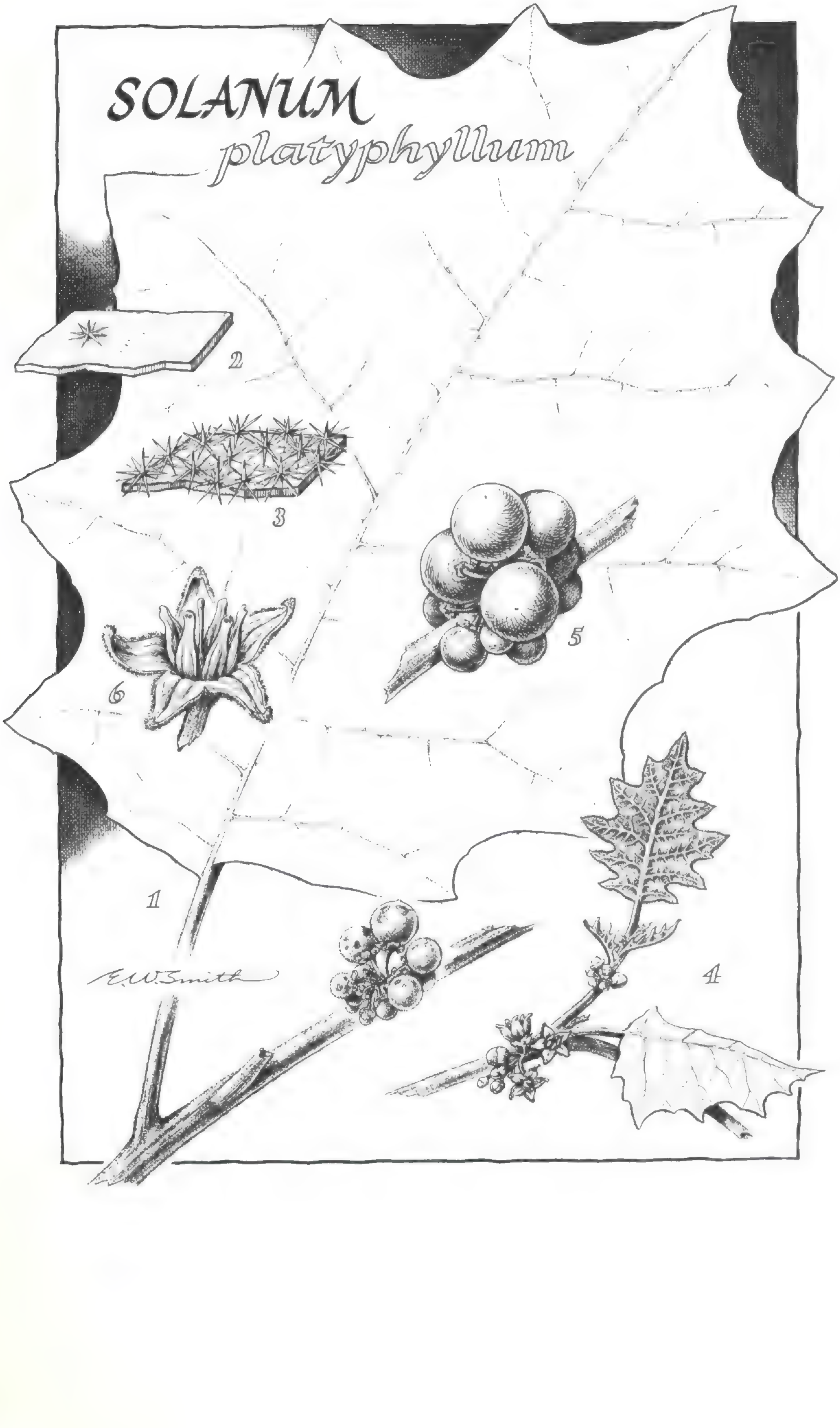
Solanum quitense Humboldt, Bonpland & Kunth Nov. Gen. & Sp. 3 (1818) 25.

Shrub unarmed, robust, rank, up to 5–7 feet tall (rarely taller). Branches stout, terete, densely soft stellate-pubescent; wood soft. Twigs densely soft-pubescent. Leaves coarsely membranaceous, usually oblong-ovate in outline, at maturity up to about 50 cm. (usually 35–40 cm.) long, 32 cm. wide, basally clasping and cordate, apically abruptly acuminate, marginally distantly, deeply and regularly sinuate, strongly petiolate (petiole terete, up to about 15–18 cm. long, densely and softly stellate-pubescent); upper surface white stellate-pubescent; nether surface softly and very densely stellate-pubescent,

EXPLANATION OF THE ILLUSTRATION

PLATE XLII. SOLANUM PLATYPHYLLUM *H. & B.* 1, fruiting branch and leaf, approximately one half natural size. 2, portion of upper surface of leaf, greatly enlarged. 3, portion of nether surface of leaf, greatly enlarged. 4, young leaves and flowers, approximately one half natural size. 5, cluster of fruits, approximately one half natural size. 6, flower, approximately twice natural size.

Drawn by ELMER W. SMITH


SOLANUM
platyphyllum
2
3
6
5
1
4
E.W.Smith

with two sizes of stellate hairs occurring together; veins pinnate, more or less 10 on each side, midrib and lateral nerves conspicuous on both surfaces but especially so beneath; blade dark green above, pale green with definite purplish hue beneath. Inflorescence a lateral, very short-peduncled, few-flowered cyme. Flowers pedicellate, white, about 4 cm. in diameter; pedicels stoutish, up to 15 mm. long, densely tawny-purple stellate. Calyx lobes suberassulent, more or less triangular, apically subacute, up to about 11 mm. long, basally 8 mm. wide, extremely densely purple-white stellate pubescent without, glabrous within. Corolla thick, membranaceous, white, lobes oblong-ovate, up to about 10–11 mm. long, 4–5 mm. wide, apically obtuse to occasionally subacute, glabrous within, densely white stellate-pubescent without. Anthers yellow, erect, linear, about 8 mm. long. Ovary globose, densely white-stellate. Fruit globose, rarely round-ovate, about 5 cm. in diameter, orange-colored when ripe, densely covered with easily deciduous white stellate hairs. Pulp acidulous, pale yellowish green. Seeds very numerous, flat, oval in outline, about 4 mm. long, yellowish white.

COLOMBIA: No definite locality. 1842, *Sinclair s.n.* Comisaría del Putumayo, Valley of Sibundoy, Sibundoy, altitude about 2225 m. "Kamsá name = *ma-sha-kve.*" February 16, 1941, *R. E. Schultes 3271.* — Same locality. May 29, 1946, *R. E. Schultes & M. Villareal 7616.* — Departamento del Huila, San Agustín, Parque Arqueológico, altitude 1600–1700 m. Nombre vulgar = *naranjilla.*" November 29, 1957, *R. Romero-Castañeda 6595.* — Comisaría del Putumayo, road from San Francisco to Mocoa, altitude about 2500 m. "Leaves purplish beneath. Flowers white. Cultivated. *Naranjilla.*" July 27, 1960, *R. E. Schultes 22549.*

Solanum quitoense, native apparently to Ecuador, grows best on the high, rainy but well drained slopes of Andean valleys between 4500 and 7500 feet, from southern Colombia to northern Peru. The plant requires about sixty inches of rain a year (McCann, L. P.: "Ecuador's

naranjilla—a reluctant guest" in Agric. Americas 7 (1947) 146–149). In Colombia, it seems to be found from Popayan southward, but a northern variety with spines is found from El Valle north and into Venezuela. In Colombia, it is not grown in any commercial quantities save in Nariño: the *naranjillo* or *lulo* may be found in abundance throughout the year in the native market in Pasto.

Solanum quitoense is cultivated on a large scale chiefly in Baños in El Topo region of Ecuador (Chalons, M. E. R. "Naranjillas—the golden fruit of the Andes" in Agric. Americas 4 (1944) 110–112). It is planted about 255 to an hektar and bears for fourteen to twenty-four months. The annual yield per hektar has been estimated as 12,500 gallons of juice and the "production of 2,000 tons of fruit requires not more than 100 hektars (about 24.7) acres of land."

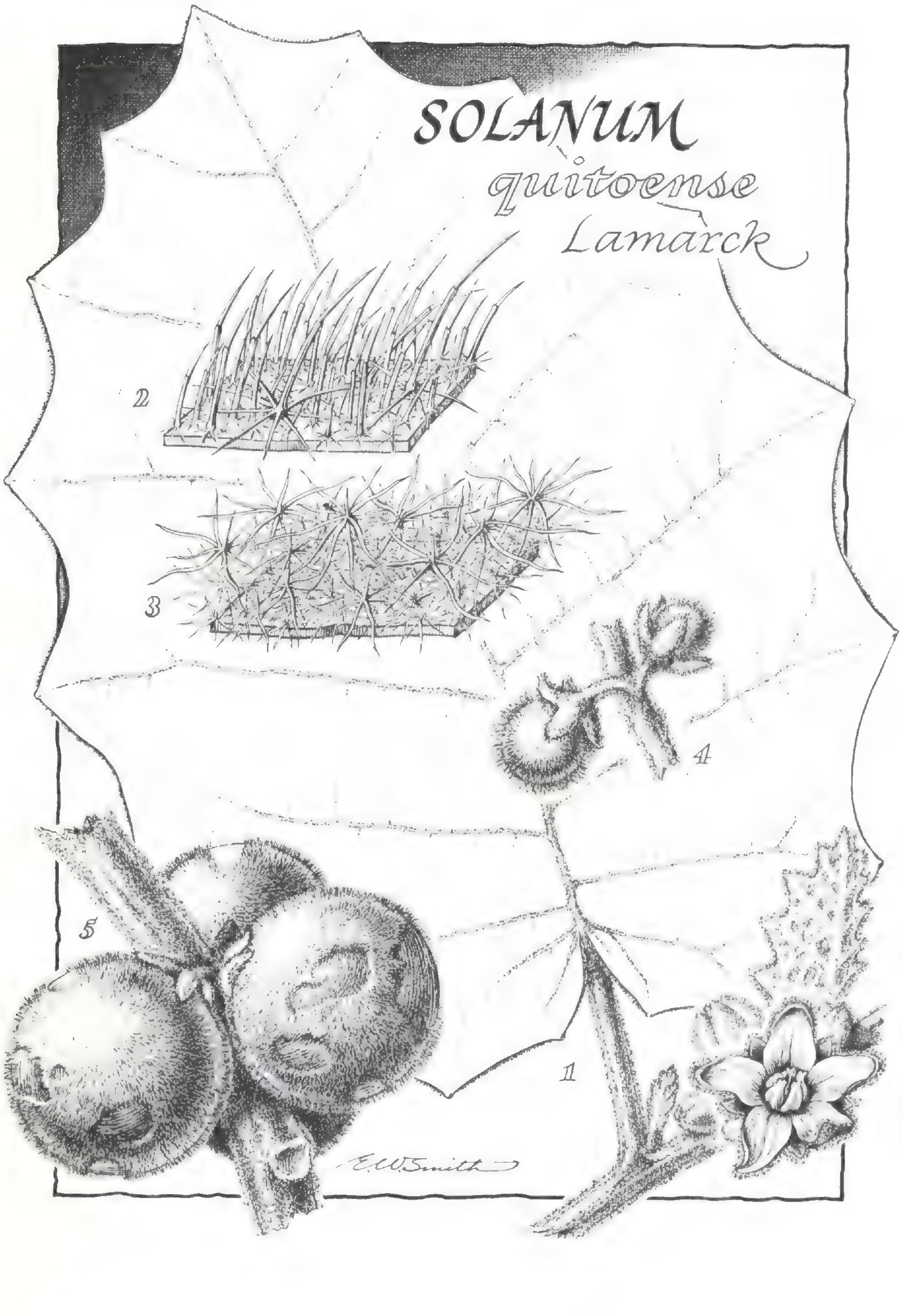
Hodge has postulated that, while *Solanum quitoense* dates certainly from pre-Spanish times, it is a relatively new arrival on the scene of cultivated plants (Hodge, W. H.: "Naranjillas or 'little oranges' of the Andean highlands" in Journ. N.Y. Bot. Gard. 48 (1947) 155–159). His main argument for this thesis stems from the absence of the *naranjillo* from pre-Columbian plant remains in ancient Peru. It is true that *Solanum quitoense* may not have been known to the Incas of Peru, but we must bear in mind that this plant must have a long association with man and agriculture, inasmuch as it is apparently no longer found in a wild state.

The fruit of *naranjilla*, so called because its color matches that of the orange, is not eaten directly but is prepared in a *sorbete* or drink. Sugar must be added because the flavor is rather tartly acid. The drink is beaten into a foamy consistency when served. The freshly squeezed light greenish juice is rich in pepsin and albu-

EXPLANATION OF THE ILLUSTRATION

PLATE XLIII. SOLANUM QUITOENSE *Lamarck*. 1, flowering branch, approximately one half natural size. 2, portion of upper surface of leaf, greatly enlarged. 3, portion of nether surface of leaf, greatly enlarged. 4, young fruits, approximately one half natural size. 5, mature fruits, approximately one half natural size.

Drawn by ELMER W. SMITH


SOLANUM
quitoense
Lamarck
2
3
4
5
1
E.W.Smith

men, proteins (up to 1.5%) and minerals (especially lime, magnesium and phosphate varying from .98% to 1.6%) (Gattoni, L. A.: "La naranjilla (*Solanum quitoense*)" Serv. Interam. Coop. Agric., Min. Agric. Com. Industr. Panama (April 1957). The taste of the juice, when sweetened, has been likened to a combination of orange, pineapple and tomato.

Attempts have been made to cultivate *Solanum quitoense* outside of its native range, but they have not been successful except in Guatemala. A recent cytological study indicates the occurrence of structural heterozygosity in the species which might be of advantage for adapting the plant to tolerance of wider ecological conditions.

Solanum quitoense *Lamarck* var. **septentrionale** *R. E. Schultes & Cuatrecasas* in Bot. Mus. Leafl. Harvard Univ. 16 (1953) 100, t. 17.

Shrub differing from *Solanum quitoense* primarily in having spines and spinules on the branches, petioles and nerves of both surfaces of the leaf.

It seems that typical *Solanum quitoense* is confined to Ecuador and southern Colombia. It is completely devoid of spines. Specimens from the northern periphery of the range of this species, however, are, with one exception, variously spiny. In all other respects even to the purplish hue of the indumentum—the northern material is indistinguishable. There is great variation in the abundance and size of the spines. This condition does not argue against the separation as a distinct variety of the spiny from the unarmed variants, because *Solanum* tends to be extremely variable in respect to spines *where they occur*.

Of interest in this connection is the fact that the Mutis collection of water-colors of Colombian plants, executed between 1783 and 1808 and which are preserved in the

Jardín Botaníco in Madrid, has plates of the two concepts *Solanum quitoense* and *S. quitoense* var. *septentrionale*. Plate 38 in volume 19 depicts one drawing of a flowering branch with a floral dissection and one with a fruiting stem and dissected fruit; this is the unarmed *Solanum quitoense*. Plate 39 shows a leafy branch in flower and one piece of stem in fruit; the stems, petioles and veins are armed with spines.

Colombia: Departamento de Antioquia. No date. *Jervisse s.n.* Itaquí, July 1944, *Br. Daniel 3352.* Alrededores de Medellín, Río Negro, altitude about 1560 m. "*Lulo.* Cultivated." February 11, 1946, *W. H. Hodge 6712.*—Departamento de Magdalena, Santa Marta, altitude 6000 ft. January 1903, *H. H. Smith 1853.*—Departamento de Santander, vicinity of California, altitude 3000 m. "*Tumo.* Shrub 4–6 ft. Corolla light blue, anthers yellow. Open hillside. January 11–27, 1927, *E. P. Killip & A. C. Smith 16949.*—Vicinity of Charta, altitude 2000–2600 m. "Shrub 4–6 ft. Corolla white, blue at margin; anthers yellow." February 1–11, 1927, *E. P. Killip & A. C. Smith 18913.*—Departamento de Cundinamarca, cercanias de San Bernardo hacia Sasaima, altitude 1600–1800 m., June 23, 1940, *J. Cuatrecasas 9604.*—Departamento del Norte de Santander, near Ocaña, January 1878, *Kalbreyer 543.*—Departamento del Tolima, Ibagué, 1844, *J. Goudot s.n.*—Departamento del Valle de Cauca, La Paila, April 1853, *Holton 23.*—Cordillera Occidental, vertiente occidental, hoya del Rio Digua, lado izquierdo, Piedra de Moler, altitude 1050 m. "*Lulo de perro.*" August 19–28, 1943, *J. Cuatrecasas 15031.*—Cordillera Occidental, vertiente oriental, Quebrada del Tigre, Quebradita de Pultabrava, altitude 1440 m., October 28, 1946, *J. Cuatrecasas 22694.*—Cordillera Occidental, vertiente occidental, hoya del Río Digua, Río San Juan, abajo de Queremál a la derecha del río entre km. 52 y 53, altitude 1300–1500 m. "*Lulo morado.*" March 19, 1947, *J. Cuatrecasas 23853.*—Cordillera Occidental, vertiente occidental, hoya del Río Digua, lado derecho, entre Queremál y La Elsa, altitude 1200–1160 m. "*Lulo.*" March 27, 1947, *J. Cuatrecasas 23992.*

Solanum sessiliflorum *Dunal* Sol. gen. aff. syn. (1816) 43.

According to Ducke (Ducke, A.: "Plantas de cultura precolumbiana na Amazônia brasileira. Notas sôbre as especies ou formas espontaneas que supostamente lhes teriam dado origem" Bol. Téen. Inst. Agron. Norte,

no. 8 (1946) 9), *Solanum sessiliflorum*, known as *cubíu*, is common in the Brazilian Estado do Amazonas, especially in its westernmost part along the Solimões River, where it is found both cultivated and wild. The fruits are said to be edible. There is, he states, another species of Solanum with small, edible fruits also known as *cubíu* along the Solimões; we believe that this species, which Ducke did not identify, may possibly be *Solanum platyphyllum*.

Sendtner (in Martius Flora Brasiliensis pt. 6 (1846) 73) cited *Solanum sessiliflorum* from Pará, at the mouth of the Amazon River, under the common name *cubio*.

We have no evidence that *Solanum sessiliflorum* is cultivated in Colombian territory, but it naturally must be expected there if it be common in the western part of the Brazilian Amazon.

It should be pointed out that the vernacular Ñengatú name *cubiyú* is applied in the Colombian Vaupés to several species of Solanum: *S. laximitante*, *S. straminifolium*, *S. Topiro;* it seems to be a rather generic name used for a number of species of Solanum with edible fruits. Near Mitú, there is a river, an affluent of the Vaupés, called Río Kubiyú.

Solanum sisymbrifolium *Lamarck* Illustr. 2 (1797) 25.

Herb up to 3 ft. tall, rank, heavily armed throughout with spines. Branches spiny. Twigs beset with stout orange or yellow spines up to 7 mm. long or longer and with distant, whitish, stipitate, stellate hairs. Leaves membranaceous, oblong or ovate, sinuately lobed or very deeply pinnatifid with sinuate or deeply dissected lobes, usually up to 12 cm. long (without petiole), 8 10 cm. wide (petiole 2 5 cm. long, with spines and stellate hairs similar to those of twigs); upper surface subdensely and coarsely stellate-pubescent, with long yellow spines along

nerves; nether surface similarly spinose and densely stellate-pubescent. Inflorescence a terminal or soon lateral raceme, few-flowered (axis strongly spinose). Flowers numerous, pale bluish, white or sometimes pale violet, about 2 cm. in diameter. Calyx lobes externally very densely spinose and sparsely stellate-pubescent, subglabrescent within, persistent in fruit, lobes narrowly triangular, apically acute, up to 8–10 mm. long, lengthening to 20 mm. with ripening of fruit. Corolla membranaceous, up to about 20 mm. long, externally golden-stellate, internally glabrous. Anthers yellow, erect, linear, about 14 mm. long with flattened filaments 4 mm. long. Ovary globose. Fruit globose, red or red-brown, up to 2.5 cm. in diameter.

COLOMBIA: Departamento de Antioquia, Abejorral, altitude 2150 m. "Nombres vulgares: *tapaculo; uchuba colorado; mancadera.*" February 1852. *J. Triana 3855/5.*—Departamento de Boyaca, Valle de la Candelaria, Municipio de Ráquira, altitude 2619 m. "Nombre vulgar: *pomas de perro.*" March 1941. *A. Ranghel Galindo 98.*—Departamento del Cauca, between Popayán and Puracé, crossing Río Anambio, altitude 2500 m. July 10, 1939. *E. Pérez-Arbeláez & J. Cuatrecasas 5860.*—Tres Cruces, vicinity of Popayán. November 6, 1948. *S. Yepes Agredo, J. Araque Molina & F. A. Barklay 18Ca015.*—Cordillera Occidental, eastern slopes, Chiquio, 21 km. NW of El Tambo, altitude 1700–1900 m. September 30, 1954. *A. Fernández Pérez 2732.*—Departamento de Cundinamarca, La Cabrera, Pandi. July 1930. *E. Pérez-Arbeláez 615.*—Fusagasugá, below town on road passing Hotel Sabaneta near Río Chocho. June 5, 1942. *G. Gutiérrez V. & R. Jaramillo M. 320.*—Departamento de Magdalena, Pozos de Agriacoca." Herba de 0.7 m. Corola blanco-lila. Frutos verdes. May 16, 1951. *R. Romero-Castañeda 8919.*—Departamento de El Valle, Cali. May 3, 1935. *H. García-Barriga 4369.*—Vicinity of Cali, altitude 1000 m. "Nombre vulgar: *uva de perro.*" July 1938. *J. M. Duque-Jaramillo 4104.*—Monte Frío, Yanaconas, altitude 17–1850 m. February 27–March 1, 1939. *E. P. Killip & H. García-Barriga 33732.*

This species is native to tropical America at higher elevations, but it is naturalized in waste ground in the West Indies and southeastern United States.

In Colombia, where it has a large number of vernacular

names, it grows subspontaneously and is semi-cultivated along roadsides and the edges of cultivated land.

Solanum straminifolium *Jacquin* Misc. 2 (1781) 298.

Shrub up to about 6 ft. tall. Trunk and basal parts of woody branches and branchlets heavily armed with spines. Leaves membranaceous, dark green above, grey-green (in life) beneath, ovate in outline, up to about 30 cm. long, 16–25 cm. wide, basally unequally truncate, apically acute, marginally very deeply sinuate, strongly petiolate (petiole up to 9 cm. long, 0.5 cm. in diameter, armed with strong spines protruding at right angles, sparsely stellate); upper surface very remotely stellate-pubescent, otherwise subglabrous; nether surface very densely white-stellate; veins conspicuous, armed above and below with relatively stout spines. Inflorescence a lateral, stout-pedunculed, few-flowered cyme (pedunculs up to 1.3 cm. long). Flowers pedicellate, pedicels up to 8 mm. long, white-stellate-pubescent. Calyx cup-shaped, leathery, inconspicuously 5-dentate, up to 3 mm. long, glabrous within, densely yellow- or white-stellate without. Corolla white with oblong lobes up to 9 mm. long, apically subacute, glabrous within, extremely densely white-stellate without. Anthers erect, yellow, linear, usually shorter than corolla. Style clavate, up to 4.5 mm. long. Ovary densely stellate. Fruit globose, up to about 3 cm. in diameter, red, densely and very minutely stellate but subglabrescent when ripe. Seeds numerous.

Colombia: Comisaría del Vaupés, Río Piraparaná, altitude 250–600 m. "Arbusto de 2 m. Flores blancas." August 27–31, 1952. *H. García-Barriga 14256*.—Río Vaupés, Cachivera de Yurupari, altitude 400 m. "N. v. *cobuía* (Kubeo). Yerba 1 m. Flores blancas; frutos rojos." October 24–26, 1952. *H. García-Barriga 14946*.

It would seem that the collections cited above may be referred to *Solanum straminifolium*, although much more

research needs to be done to ascertain exactly the specific limits of this concept. It is closely allied to *Solanum liximitante:* the differences were discussed above under *S. liximitante.* If the limits of the apparently rather widespread *Solanum straminifolium* can be resolved, *S. liximitante* may perhaps deserve but varietal rank. At the present time, however, it appears to be wiser to recognize them as distinct. They are distinct in the field, and the Indians of the Vaupés of Colombia easily point out the differences, recognizing them occasionally by the use of slightly different common names for the two. There may, however, be natural hybridization in some localities where both have been grown for long periods together.

Solanum straminifolium grows in the lowland, tropical forest regions of Amazonian Colombia, never passing 1500 feet above sea-level. The natives of this area not only eat the fruits but put them in vinegar for pickling and to use as condiments in other foods. It is called *e-to-pa-a* in Tukano of the Vaupés (Romero-Castañeda loc. cit. 288) and, amongst the Kubeos of the same area, the name *ko-bu-yá* is employed.

Solanum Topiro *Humboldt & Bonpland ex Dunal* Sol. gen. aff. syn. (1816) 10.

Shrub unarmed, robust, rank, up to about 5 ft. tall. Branches stout, terete, scurfy-pubescent, grey-green in life. Twigs densely white-stellate-tomentose. Leaves coarsely membranaceous, ovate in outline, at maturity up to about 48 cm. long, 36 cm. wide, basally inequilaterally truncate, apically abruptly acute, marginally very distantly and very deeply sinuate, strongly petiolate (petiole up to 12 cm. long, densely white-stellate-tomentose); upper surface coarsely tomentose and densely clad with somewhat stiff, sericeous white hairs (some of which have basally a stellate formation) sparsely inter-

spersed with white-stellate hairs; nether surface very softly and densely white-stellate-tomentulose; veins strong and conspicuous above and below, extremely densely white-stellate-tomentose. Inflorescence a lateral, very short-pedunculed, few-flowered cyme. Flowers pedicellate; pedicels up to 6 mm. long, 1.5–2 mm. in diameter, very densely stellate-tomentulose. Calyx lobes somewhat crassulent, more or less triangular-ovate, apically subacute, up to about 15 mm. long, very densely and softly greyish brown-stellate-tomentose without, glabrous but with minute white scabs within. Corolla membranaceous, white or greenish white, lobes oblong-ovate, up to about 20 mm. long, apically subacute, glabrous within, densely stellate-tomentulose without. Anthers yellow, erect, linear, about 9–10 mm. long. Style terete, 7–8 mm. long. Ovary globose, very densely long-white-sericeous. Fruit subglobose to ovoid, up to 4.5 (possibly 5) cm. in diameter, ripening orange-red, sometimes tomato-red, densely and minutely stellate-tomentulose (hairs easily caducous upon handling), becoming subglabrous upon ripening. Pulp acidulous. Seeds very numerous, flat, oval in outline, 3–4 mm. long, 2–2.5 mm. wide, pale yellowish.

COLOMBIA: Comisaría del Amazonas, Río Caquetá, vicinity of La Pedrera. April 1944, *R. E. Schultes 5881.*—Río Loretoyacu, altitude about 100 m. September 1946, *R. E. Schultes & G. A. Black 8394.*—Río Apaporis, Soratama, near mouth of Río Kananarí. "*Lulo. Topirú.* Fruit ovoid, orange, covered with hair in unripe stage. Cultivated. Flowers whitish with yellow anthers." March 1951, *R. E. Schultes 12081.*—Same locality. "Kubeo=*be-tá-ka.* Taiwano=*de-twá.* Tatuya =*de-twá.* Cultivated." September 1, 1951, *R. E. Schultes & I. Cabrera 13842.*—Comisaría del Putumayo, Río Putumayo, Puerto Asís. "Shrub up to 3 ft. Fruit orange-red, covered with caducous hairs. Leaves and petioles spineless. "*Lulo. Cocona.*" August 2, 1960, *R. E. Schultes 22571.*—Comisaría del Vaupés, Río Vaupés, Mitú. *H. García-Barriga, R. E. Schultes & H. Blohm 15771.*

In the Vaupés and Amazonas of Colombia, the following Indian names are used for *Solanum Topiro:* Karapana

Plate XLIV

Plate XLIV. Solanum Topiro *H. & B.* Flowering branch of the plant from which *Schultes 12081* was collected.

Photograph by Richard Evans Schultes

PLATE XLV. SOLANUM TOPIRO *H. & B.* 1, flowering branch, with medium-sized leaf, about one half natural size. 2, portion of the upper surface of the leaf, greatly enlarged. 3, portion of the nether surface of the leaf, greatly enlarged. 4, inflorescence, about one half natural size. 5, fruits, about one half natural size. 6, young leaf, about one half natural size. *Drawn by* ELMER W. SMITH

Plate XLVI

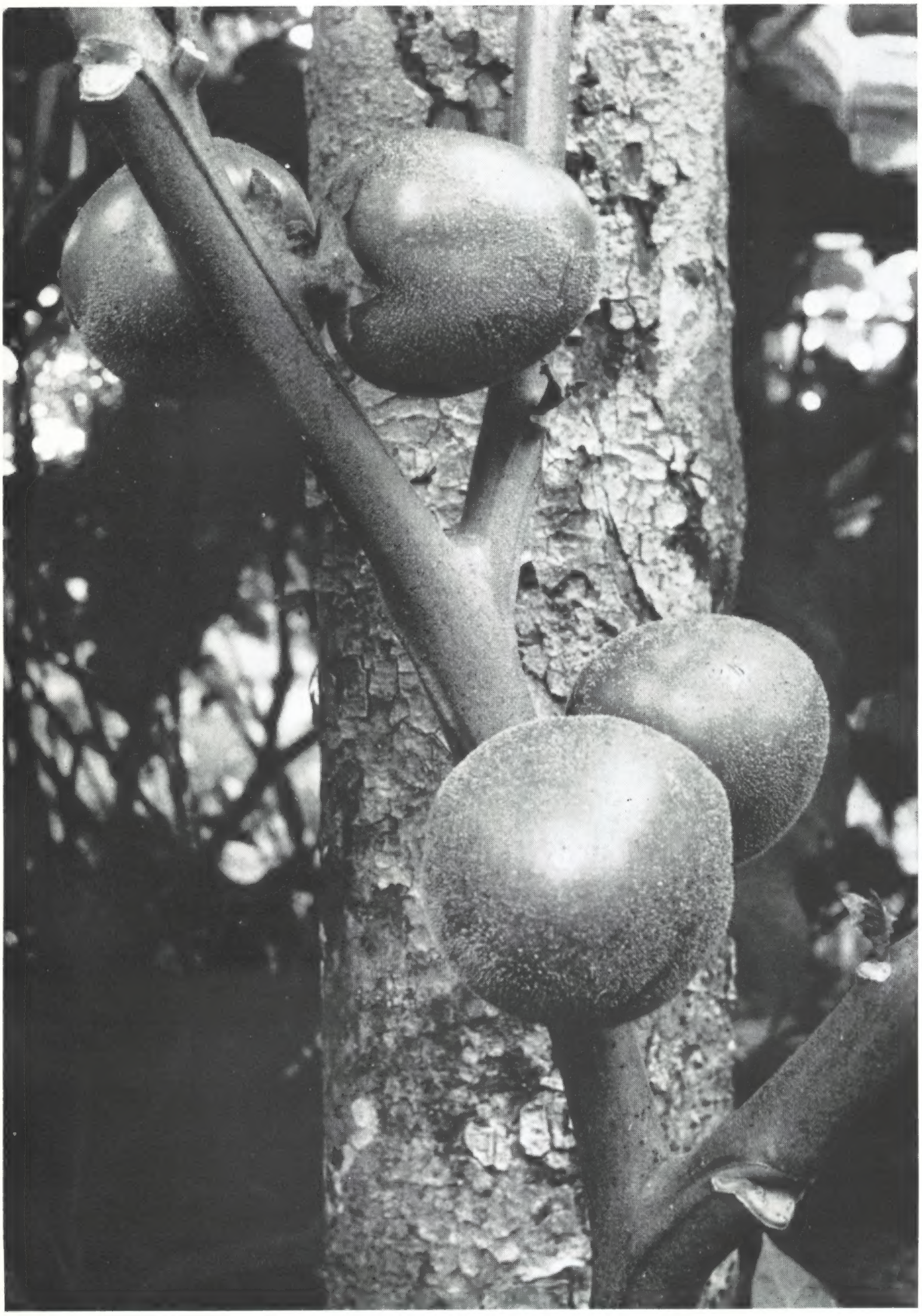


Plate XLVI. Solanum Topiro *H. & B.* Fruiting branch of the plant from which *Schultes 12081* was collected. *Photograph by* Richard Evans Schultes

(Río Kananarí)—*lĕ-tó;* Karijona (Río Caquetá)—*ho-moo-mé;* Kuripako (Río Guainía)—*ma-ré-da;* Makú (Río Piraparaná)—*bĕ-beñ;* Makuna (Río Apaporis)—*ma-rá;* Miraña (Río Caquetá)—*ró-ya;* Puinave (living on Río Apaporis)—*pooḿ-ka;* Taninuka (Río Popeyacá)—*ba-rá;* Yukuna (Río Miritiparaná)—*po-ró-la.*

An examination of the major works on tropical fruit plants indicates that *Solanum Topiro* has been completely neglected and probably unknown as a cultigen. As Fennell (Fennell, J. L. "*Cocona*—a desirable new fruit" in For. Agric. 12 (1948) 181) has written: "To what extent, if any, the *cocona* [*Solano Topiro*] may have reached the gardens of the outside world is difficult to say. That it appears even now to be essentially unknown to horticulture leads me to believe, in light of its impressive appearance and apparent usefulness, that it may never have previously left its secluded habitat as a recognized fruit of value."

The first serious attention paid by botanists to *Solanum Topiro* as a cultigen dates from the middle of the 1940's. During this period, seeds of the plant were collected "from the little-explored reaches of the upper Amazon" (presumably in Peru) and established in the Experiment Station at Tingo María in Peru. Eventually, it was introduced to the Instituto Interamericano de Agricultura Tropical in Turrialba, Costa Rica, loc. cit.; Ochse, J. J. "*Solanum hyporhodium* or *cocona*" in Proc. Fla. State Hort. Soc. 66 (1953) 211), from which centre it began to attract horticultural attention.

The vernacular name for *Solanum Topiro* in Peru is reported to be *cocona*. This is borne out by notes on herbarium specimens (*Killip & Smith 27367, 27823*) collected in the Amazonian part of Peru in 1929. In the Putumayo region of Colombia, the plant has two vernacular names —*cocona* and, amongst the settlers recently arrived from

Plate XLVII

Plate XLVII. Solanum Topiro *H. & B.* Fruiting branches of the plant from which *Schultes 22571* was collected. *Photograph by* Richard Evans Schultes

highland Colombia, *lulo*. The convenient epithet *cocona* followed the plant in its several introductions and has now, in the literature, been accepted as a standard common name. Unfortunately, however, *cocona* was erroneously identified and, in agricultural institutions as well as in the scientific and popular literature, was determined as representing *Solanum hyporhodium* A. Br. et Bouché. This error was corrected in 1958 (Schultes, R. E.: "A little known cultivated plant from northern South America" in Bot. Mus. Leafl. Harvard Univ. 18 (1958) 229–244).

Solanum Topiro has never apparently been collected from the wild, and we have never seen it outside of agricultural plots or abandoned house-sites which obviously had been the scene of cultivation. We probably have at hand in this plant a species so long in association with man that it may nowadays exist only because of this association. The fruit yields viable seeds in great abundance, but the plants seem to reproduce themselves only in highly disturbed and sunny sites.

The Indians eat the ripe fruit as a tomato. The civilized inhabitants of the region use the fresh fruits to prepare, with sugar, a rather acidulous, thirst-quenching drink. The plant is apparently never set out deliberately but springs up from seeds adhering to the rind when this is cast into refuse heaps or when inedible parts of the fruit are spat out in the process of eating. The species is grown over a wide area including much of forested eastern Peru, most of the Amazon drainage-area of Colombia, the upper reaches of the Orinoco system in Venezuela and probably to a much lesser extent adjacent parts of Brazil.

We gratefully acknowledge important help in bibliographic matters from Mrs. Julia Morton of the Morton Collectanea.